



# Vascular plant and ground beetle diversity on wet arable land versus conventional crop fields

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## Abstract

While artificial farmland drainage has allowed the development of a highly productive agriculture, the availability of periodically flooded arable land as a niche habitat for a broad range of animal and vascular plant species has diminished. Accordingly, many species depending on temporary wetlands are endangered, already extinct or extirpated in Switzerland and other European countries. Some arable fields with temporary pools can still be observed in Switzerland. However, it is not known how suitable such small temporary ponds are as habitats in the modern, intensively-managed agricultural landscape, where disturbance rates are high, and connecting wetland habitats are scarce. We surveyed 120 fields across 10 hot spot regions for potential waterlogging in Switzerland, investigating the effect of temporary waterlogging on the diversity of arable plant and ground beetle species. Half of the fields were heavily influenced by waterlogging, while the other half represented conventional crop field controls. We found that wet fields exhibited a higher number of vascular plant and carabid species on average compared to control fields. This difference was explained by the presence of more hygrophilic plant and ground beetle species on wet fields. While we did find more hygrophilic species on wet fields, the threatened character species of temporary wetland habitats were mostly absent despite availability in regional species pools. These results suggest that temporary pools still provide the raw environmental characteristics that hygrophilic species require in the agricultural landscape. However, alternative management schemes are required to transform them into habitats that can effectively support high-priority, threatened species of temporary wetlands.

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## Introduction

While temporary waterlogging of agricultural soils used to be widespread in the European agricultural landscape, such natural phenomena have become rare. Wherever

possible, sites with temporary ponds were artificially drained by drainage installations or lost as a consequence of major river corrections (Davies et al., 2008; Gramlich, Stoll, Stamm, Walter & Prasuhn, 2018; Hefting, van den Heuvel & Verhoeven, 2013; Williams, 1997; Wood, Greenwood & Agnew, 2003). In Switzerland, like many other European countries, most agricultural drainage installations were established over the past 200 years, with construction

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peaking during the Second World War amidst efforts to obtain national food security (Béguin & Smola, 2010; Gimmi, Lachat & Bürgi, 2011; Zollinger, 2006). An estimated 18% of Switzerland's agricultural land is artificially drained (Béguin & Smola, 2010) and it is probably the most relevant cause for wetland loss (Fischer et al., 2015; Grünig, 1994; Lachat et al., 2010).

Such investments allowed the development of a highly productive agriculture, but this came at the cost of losing niche habitats for a broad range of animal and vascular plant species (Hefting et al., 2013; McLaughlin & Mineau, 1995). Next to the loss of the habitats themselves, the loss of connectivity between wet habitats due to widespread agricultural drainage further contributed to the loss of wetland biodiversity (Gimmi et al., 2011). Accordingly, many species depending on periodically waterlogged habitats are endangered or have already become extinct or lost in Switzerland and other European countries (Altenfelder, Raabe & Albrecht, 2014; Delarze et al., 2016; Moser, Gyax, Bäumlér, Wyler & Palese, 2002). The *Nanocyperion* and *Bidention* plant sociological societies are especially endangered (Delarze, Gonseth, Eggenberg & Vust, 2015). These societies are in decline in Switzerland, occurring now mainly as fragments in the warm and humid, low-lying locations outside of the Alps (Delarze et al., 2015). The same applies to many animal species, e.g., amphibians are among the most endangered species group in Switzerland (Cordillot & Klaus, 2011; Griffiths, 1997) and many carabid beetles of wetland habitats have an increased risk of extinction (Nolte, Boutaud, Kotze, Schultdt & Assmann, 2019).

Wet arable land (WAL), i.e. cropland with small temporary ponds, receives little attention in the literature and is often neglected in biodiversity assessment (Blackwell & Pilgrim, 2011; Lukács, Sramkó & Molnár, 2013). Possessing hydric soils periodically inundated with water, WAL meets most definitions of wetlands (Cowardin, Carter, Golet, & LaRoe, 1979). Likely due to their small size and fleeting nature, they are, however, absent from most national wetland inventory systems (Blackwell & Pilgrim, 2011). They are generally characterized by local, seasonal flooding, typically in spring, which is followed by an extended drying out period (Lukács et al., 2013).

The locations of such ponds before draining activities started are poorly documented. A map locating potential hot-spots of WAL in Switzerland was recently developed (Szerencsits et al., 2018). It identifies areas where waterlogged soils are expected under natural conditions. The map considers local topography and geological characteristics, soil-water balance, and observations of wetlands in historical maps. However, it gives no information about the water balance under current use; it may, therefore, only be used for an estimation of the potential for waterlogging. High potential locations in this map represent compelling opportunities for enhancing the biodiversity value of arable land

through restoration of sites with an indication of previous waterlogging (Alderton, Sayer, Davies, Lambert & Axmacher, 2017).

Although not widespread, WAL can still be observed in Switzerland. The main causes for the periodic flooding include drainage pipes in poor condition or elevated water levels due to the subvention of organic soils. However, it is not known how suitable such small temporary wetlands are as habitats in the modern, intensively-managed agricultural landscape, where disturbance rates are high, and connecting wetland habitats are scarce.

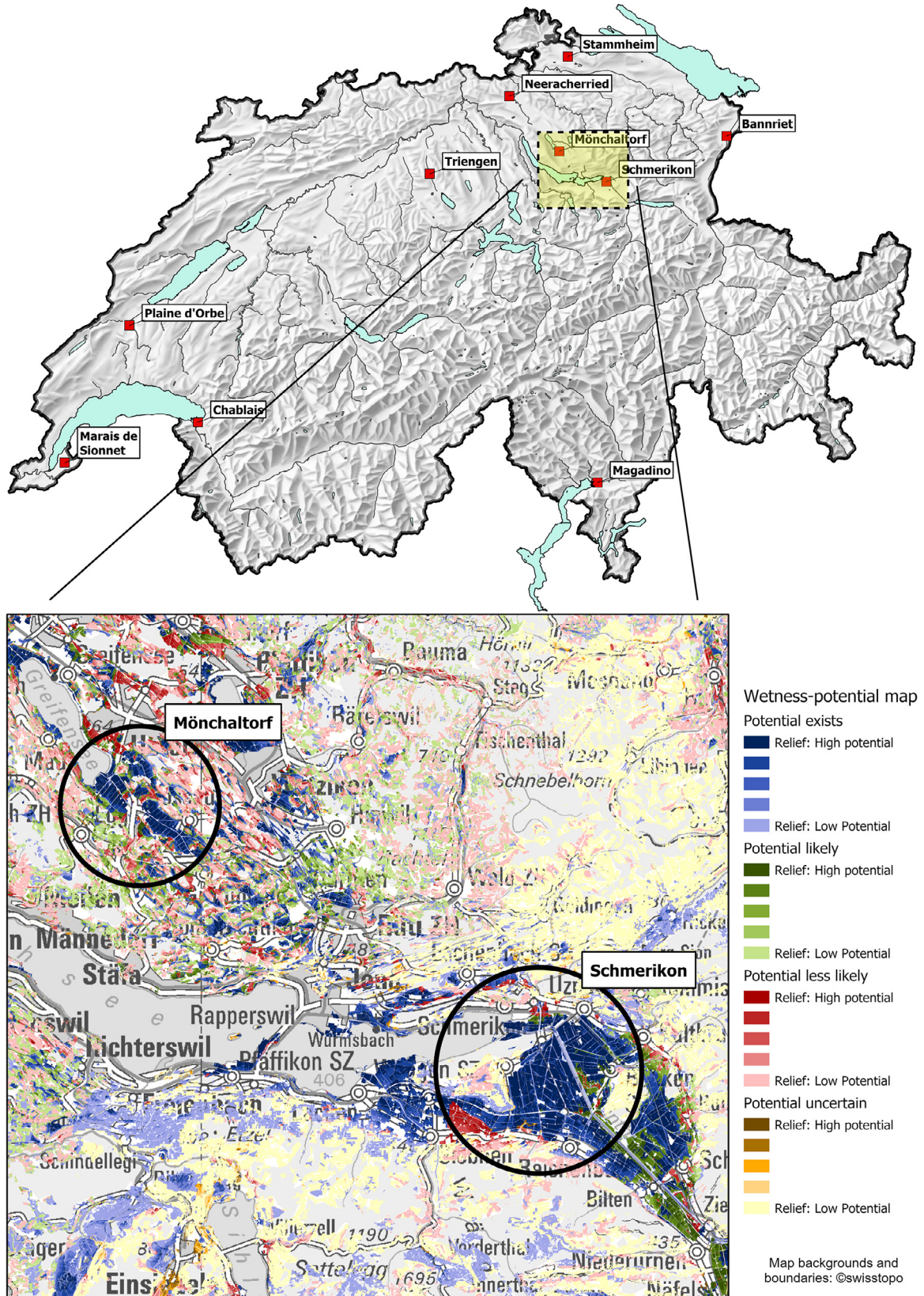
In this study, we surveyed 120 fields across 10 hot spot regions for WALs in Switzerland, investigating the effect of temporary waterlogging on the diversity of arable plant and carabid species. In each region, we sampled six fields strongly influenced by temporary waterlogging and six control fields representing conventional crop fields. The study aims to evaluate the value of WALs as habitats for vascular plant and carabid species which depend on temporary ponds in an open landscape. It further has the goal to provide a basis for the planning of biodiversity promotion on WAL.

## Materials and methods

### Site selection

Ten sample regions prone to waterlogging were selected across Switzerland using a combination of Szerencsits et al. (2018) wetness potential map and aerial photography (Fig. 1). Emphasis was placed on selecting locations where large tracts of high wetness-potential arable land coincided with nationally protected wetland sites (Fig. 1).

Within each region we selected six fields which exhibited temporary flooding (wet fields, WF) and six control fields (CF) representing well-drained, conventional arable land. Fields were selected by eye in January/February 2018 after a period of heavy rain, when pools of standing water could be observed in WFs but not in CFs (Fig. 2). In total, 60 WFs and 60 CFs were sampled. While we attempted to keep field locations close together, the size of each sample region was determined by the availability of suitable WFs. Thus, the areas covered by the sample regions varied from 1.8 to 8.1 km<sup>2</sup>, measured as the smallest convex hull around the sample fields. Due to the limited availability of WFs in some regions, WFs and CFs could not be paired following the same methodology across all regions and we refrained from later pairwise analysis. The crop types encountered across the 120 fields were grouped into 9 different categories: fallow land ( $n = 3$ ), vegetables ( $n = 7$ ), cereals ( $n = 37$ ), potatoes ( $n = 2$ ), leguminous plants ( $n = 4$ ), maize ( $n = 46$ ), oilseed rape ( $n = 9$ ), sunflowers ( $n = 2$ ), and sugar beet ( $n = 10$ ). Average, minimum, and maximum field sizes and distances between fields are recorded in Appendix A: Table 1.



**Fig. 1.** Sample region locations across Switzerland. The zoomed-in panel highlights how the wetness-potential map describes the open fields of Mönchaltorf and Schmerikon as locations with a high potential for periodical flooding (dark blue).



**Fig. 2.** Example field from the Orbe sample region with standing water in January when the sites were selected (left) and with an oilseed rape crop in July during the survey period (right). The water-logging indicates poor drainage which is reflected in the heterogeneous crop development in summer.

## Sampling method

Each field was sampled twice, in April/May and in July/August 2018. With each visit, crop cultures on each field were noted. All vascular plant species occurring within a 1 m wide margin of each field (ca. 50 cm inside and outside the field) were recorded. All fields were surveyed by the same person. Simultaneously, carabids were captured along the field margins of each site by hand with the aid of battery-powered pooters. Each field was surveyed by one person for 30 min. All sides of the field were traversed, taking care to search as many types of microhabitats as possible (vegetation heaps, soil clumps, stones, etc.). The sampling was split between two similarly experienced surveyors who rotated fields between spring and summer visits to minimize observer bias. Experienced hand-collectors have been shown to outperform pitfall traps when only species detection is required (Knapp, Jana, Jakubec, Vonička, & Moravec, 2020). Sampling was conducted only with presence/absence data in mind, i.e., where possible, a single individual per sampling site was captured for each species which was recognizable in the field. Captured individuals were preserved and later identified under light microscope following Freude, Harde and Lohse (2004). Uncertain identifications were verified by a local carabid expert (W. Marggi).

To estimate the available pool of hygrophilic carabid species detectable by hand collection within each region, additional carabid surveys were performed within neighbouring wetlands of the sample sites. We used aerial photographs to identify and visit as many distinct habitats within each wetland as possible. On each visit, a total of at least 7 h split amongst the surveyors was devoted to collection in the wetland sites of each study region. Further details on the number and sizes of sampled wetland sites can be found in Appendix A: Table 1.

## Analysis

### Effect of field type on plant and carabid diversity

Differences in plant and carabid species richness on WFs and CFs were analysed at the local and the regional scale using a generalized linear mixed effect model (GLMM) with a negative binomial error distribution and log link function suited to count data with overdispersion. Analysis was carried out in R (v4.0.2) with the function *glmer.nb* from the package ‘lme4’ (Bates, Maechler, Bolker & Walker, 2015, R Core Team, 2017). Field type (WF/CF) was considered as a fixed effect with sample region as a random intercept. We also tested for the effects of field size and crop culture by adding the former to the model as a fixed effect and the latter as a second crossed random intercept. For the analysis of local, alpha diversity, the dependent variable for each species group was per field species totals (60 replicates of WF and CF each; note that diversity as used in this paper refers only to species richness). For the regional analysis of gamma diversity, the total number of species found across all WFs and all CFs within each study region was used as the dependent variable (10 replicates each of WF and CF). Additionally, we examined differences in the turnover of species, beta diversity, across WFs/CFs by calculating Jaccard dissimilarity indices of the species assemblages found on either field type within each region using the package ‘betapart’ (Baselga et al., 2020).

We also compared the proportion of species found on WFs and CFs with respect to threatened status and water affinity. For plants, we tallied all species listed in Switzerland’s Red List (RL) as rare or threatened (R, NT, V, EN, CR; Cordillot & Klaus, 2011) per field and per region. For carabids, we adopted a custom list of species of conservation interest based upon the currently outdated Red List (Huber & Marggi, 2005; Marggi, 1994; see list in Appendix A: Table 2). The proportions of hygrophilic plants were also compared. Plants were classified from 1 to 5 following their

soil humidity ratings ( $F$ ) from Flora Indicativa (Landolt et al., 2010), where  $F = 1$  corresponds to xerophilic and  $F = 5$  to hygrophilic. All plant species with a humidity rating of 4 or higher were considered as hygrophilic plant species. We also evaluated the proportions of semi-humid plant species with a preference for strong, periodical changes in soil humidity ('Wechselfeucht' = 3 in Flora Indicativa). Similarly, carabids were classified as stenoxero-, xero-, meso-, hygro-, and stenohygrophilic following the ratings from the Eco-Fauna databank (Rust-Dubié, Schneider & Walter, 2006). Lastly, we compared the proportion of carabid species from each field type which we also sampled from nearby local wetlands. As each of these are proportional measures ranging between 0 and 1, they were independently tested as the dependent variable in a binomial GLMM with a logistic link function. Like the negative binomial GLMMs, field type was the sole fixed effect and sample region was a random intercept. The proportional response variables were weighted by the total number of plants/carabids on each field.

### Species assemblage differences

Apart from species richness, we examined the composition of species assemblages at each field. Using the 'adonis' function from the R package, *vegan* (Oksanen et al., 2018), we explored differences in the assemblages of carabid and plant species found on WFs and CFs with PERMANOVA based on the Jaccard dissimilarity measure (permutational multivariate analysis of variance, McArdle & Anderson, 2001). A matrix of species presence versus sample site was used as the dependent variable, with field type (WF/CF), crop type, and study region as explanatory variables. Using 'metaMDS', the nonparametric multidimensional scaling (NMDS) function in the *vegan* package, we created ordination plots which visualize the assemblage differences.

Lastly, indicator species associated with each site type were determined by calculating indicator values for all species using the R package, 'indicspecies' (De Caceres & Legendre, 2009; Dufrene & Legendre, 1997). Indicator carabid species could be determined for five different site types: WFs, CFs, arable (WFs + CFs), wetlands, and wet sites (wetlands + WFs). Since vascular plants were only surveyed on the sample fields, indicator plant species were only determined for WFs and CFs.

### Landscape metrics

To explore the surrounding landscape's effect on plant and carabid species richness, we examined the distances to and proportions of key land cover types around each field. Spatial data for forest and hedges, flowing and standing water, open land, roads, and wetlands were plotted alongside the sample fields in ArcGIS (ESRI, 2016) to generate these basic metrics. Land cover proportions were calculated in buffers of 50 m, a distance we assumed relevant to both

plants and carabids and which minimized the overlap of landscape metrics among nearby fields (the percent overlap of buffer areas due to nearby fields is summarized in Appendix A: Table 1). 'Distance to' metrics were not limited. See Appendix A: Table 3 for details on the spatial data. To assess the possible effect of each landscape metric on species richness, we used a multi-model averaging approach with the functions 'dredge' and 'model.avg' from the R package 'MuMIn' (Barton, 2020). The full model consisted of all landscape metrics inserted into the negative binomial GLMM that was used in the analysis of species richness on WFs and CFs. Potential models were ranked according to QAICc scores, which are suited to overdispersed count data and limited sample size (Kim, Cavanaugh, Dallas & Foré, 2013). Distances to standing water and wetlands were very strongly correlated and so the distance to wetlands measure was omitted in favour of the more prevalent standing water metric. Distance to standing water and the proportion of standing water within 50 m were not strongly correlated, and since the distance metric captures potentially relevant information that the proportion metric cannot capture (a pond being adjacent to a field, or a pond being just beyond the 50 m range), both metrics were included in the model averaging.

## Results

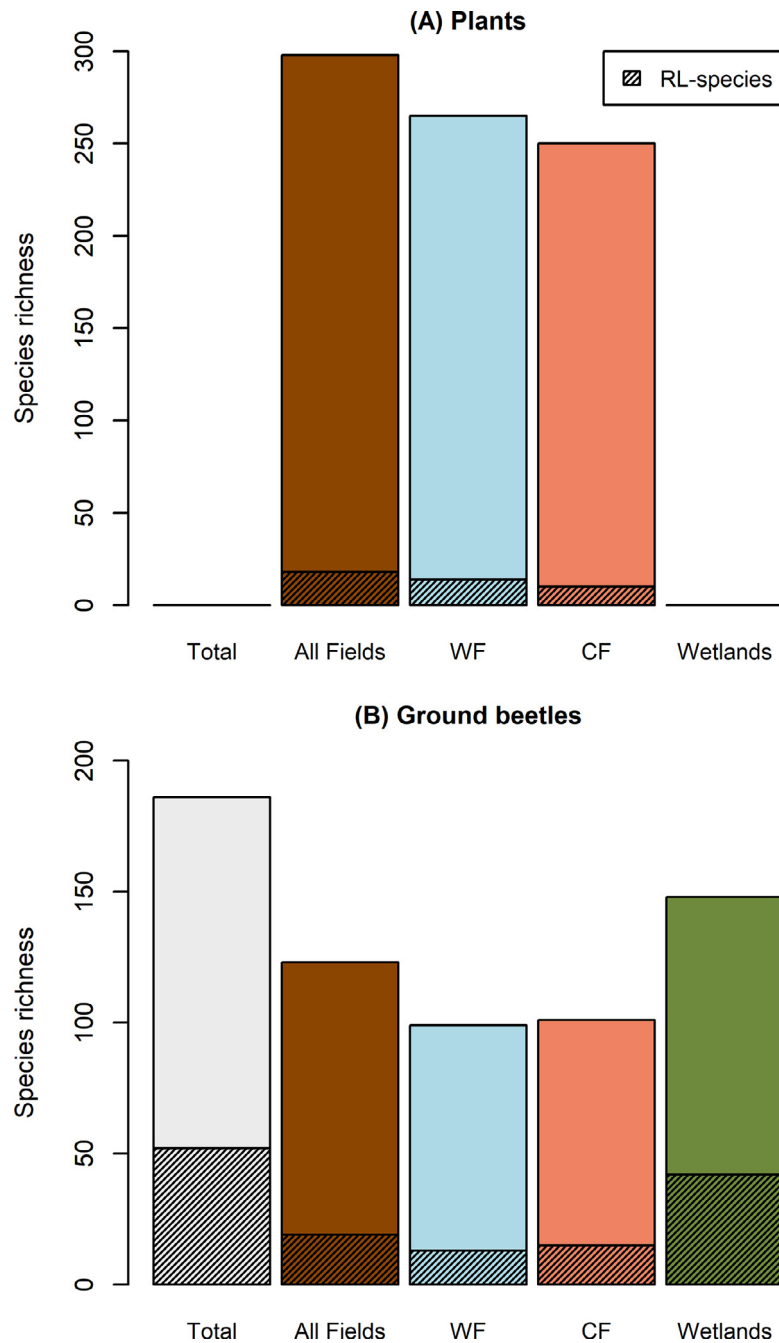
### Plant and carabid diversity

Across the entire campaign, we recorded 298 vascular plant species, with 265 occurring on WFs and 250 on CFs (Fig. 3A, Appendix A: Table 2). In total, only 18 RL plant species were observed (~6%; Cordillot & Klaus, 2011). The majority had the status "near threatened". Five plants with the status "vulnerable" were recorded (*Consolida regalis*, *Lathyrus tuberosus*, *Legousia speculum-veneris*, *Stachys annua*), and only one categorized as "endangered" (*Agrostemma githago*).

Across all sample fields on agricultural land, 123 ground beetle species were found, and a total of 186 were found after including species observed in the surrounding wetlands. 99 species were captured on WFs and 101 on CFs (Fig. 3B, Appendix A: Table 2). Nineteen carabid species of conservation interest were found on the sample fields (~15%), including highly threatened species such as *Agonum viridicupreum*, *Brachinus sclopeta*, and *Notiophilus substriatus*. The nearby wetlands, in comparison, were home to 41 species of conservation interest (~28%).

### Diversity on wet and control fields

Whether examining average per field diversity (alpha) or total regional diversity (gamma), no overall differences were detected between the number of plant or carabid species found on WFs and CFs. However, differences between WFs



**Fig. 3.** Total species observed across the entire campaign for (A) vascular plants and (B) ground beetles. Species richness is displayed over all field types (brown), on wet fields (WFs, blue), control fields (CFs, red). For ground beetles, the totals are shown for all sample sites (grey), and in nearby wetlands (green). The hatched sections of the bars represent the proportion of species of special conservation interest.

and CFs emerged after including sample region as a blocking effect in the model. With sample region included, WFs exhibited a significantly higher alpha diversity than CFs for both taxa (Table 1, Fig. 4). WF had an estimated 4.3 more plant species per field (C.I.<sub>95%</sub> = 0.6–7.2 species) and 1.7 more carabid species (C.I.<sub>95%</sub> = 0.1–3.2 species). Gamma diversity remained non-significant for both taxa. Alternatively, regional beta diversity of carabids was on average higher for CFs (0.82) compared to WF (0.80, paired *t*-test = 2.91,

*df* = 19, *p*-value = 0.009). Differences in plant beta diversity were not significant.

Crop type was moderately collinear with sample region (VIF = 2.54). And while crop type improved model outputs when added to the GLMM as the sole random effect, models with region alone performed better than those with crop type alone or with crop type and region included as two crossed random intercepts (e.g.: for plant richness: AIC<sub>Ccrop</sub> = 941.6, AIC<sub>Creg</sub> = 926.6, AIC<sub>Creg+crop</sub> = 928.2; X<sup>2</sup>-comparison of the model outputs of GLMM<sub>reg</sub> vs GLMM<sub>reg+crop</sub> = 0.60,

**Table 1.** GLMM results for the effect of field type (wet fields vs control fields) on the local diversity of plant and carabid species, and the effects of humid plant species richness on carabid diversity. Models with count data for the response variable (n) were fitted with the negative binomial distribution and a log link. Those with proportional responses ( $\hat{p}$ ) used the binomial distribution with a logit link weighted by the total number of plant/carabid species at each site.

Response	Fixed Effect	Estimate	SE	z	p	$\sigma^2_{\text{Region}}$	$R^2_{\text{Conditional}}$	$R^2_{\text{Marginal}}$
n <sub>plants</sub>	(Intercept)	3.950	0.044	89.270	< 0.001***	0.012	0.25	0.03
	TypeCF	-0.087	0.038	-2.264	0.024*			
$\hat{p}_{\text{Red List plants}}$	(Intercept)	-4.882	0.281	-17.368	< 0.001***	0.335	0.11	0.02
	TypeCF	-0.537	0.316	-1.698	0.089			
$\hat{p}_{\text{semi-humid}}$	(Intercept)	-1.142	0.093	-12.327	< 0.001***	0.068	0.02	0.00
	TypeCF	-0.115	0.062	-1.858	0.063			
$\hat{p}_{\text{F1-2}}$	(Intercept)	-1.204	0.093	-12.907	< 0.001***	0.069	0.02	0.00
	TypeCF	0.101	0.060	1.665	0.096			
$\hat{p}_{\text{F4-5}}$	(Intercept)	-3.311	0.297	-11.150	< 0.001***	0.776	0.20	0.01
	TypeCF	-0.483	0.136	-3.540	0.000***			
n <sub>carabids</sub>	(Intercept)	2.749	0.077	35.525	< 0.001***	0.044	0.34	0.03
	TypeCF	-0.117	0.056	-2.075	0.038*			
$\hat{p}_{\text{Red List carabids}}$	(Intercept)	-3.860	0.414	-9.293	< 0.001***	1.076	0.25	0.00
	TypeCF	-0.134	0.264	-0.505	0.613			
$\hat{p}_{\text{wetland carabids}}$	(Intercept)	-0.009	0.250	-0.037	0.971	0.575	0.15	0.00
	TypeCF	-0.175	0.099	-1.762	0.078			
$\hat{p}_{\text{xerophilic}}$	(Intercept)	-1.831	0.136	-13.430	< 0.001***	0.095	0.04	0.01
	TypeCF	0.341	0.128	2.671	0.008**			
$\hat{p}_{\text{hygrophilic}}$	(Intercept)	-1.341	0.153	-8.768	< 0.001***	0.167	0.06	0.02
	TypeCF	-0.483	0.125	-3.867	0.000***			
$\hat{p}_{\text{hygro. carabids}}$	(Intercept)	-1.517	0.163	-9.281	< 0.001***	0.122	0.07	0.03
	TypeCF	-0.402	0.127	-3.175	0.002**			
	$\hat{p}_{\text{F4-5}}$	4.926	1.720	2.864	0.004**			
n <sub>carabids</sub>	(Intercept)	2.714	0.086	31.617	< 0.001***	0.039	0.39	0.11
	TypeCF	-0.202	0.074	-2.732	0.006**			
	$\hat{p}_{\text{F4-5}}$	0.776	0.930	0.823	0.410			
	TypeCF: $\hat{p}_{\text{F4-5}}$	3.054	1.245	2.454	0.014*			

n: number of species

$\hat{p}_{\text{semi-humid}}$ : the proportion of plants that favour habitats with strong, periodical changes in humidity (soil humidity changes 2 or more levels on *Flora Indicativa*'s 1–5 humidity scale)

$\hat{p}_{\text{F1-2/F4-5}}$ : the proportion of plants that favour dry (F1–2) or humid (F4–5) soils (*Flora Indicativa*'s 1–5 humidity scale).

$\hat{p}_{\text{wetland carabids}}$ : the proportion of carabid species on a field which were also found in neighbouring wetlands.

$\hat{p}_{\text{xerophilic/hygrophilic}}$ : the proportion of carabid species classified as (steno-)xerophilic or (steno-)hygrophilic species in *EcoFauna Datenbank*.

$\sigma^2_{\text{Region}}$ : variance of the random intercept sample region.

$R^2$ : conditional and marginal  $R^2$  calculated based on Nakagawa, Johnson and Schielzeth (2017).

\*:  $p < 0.05$ .

\*\* :  $p < 0.01$ .

\*\*\*:  $p < 0.001$ .

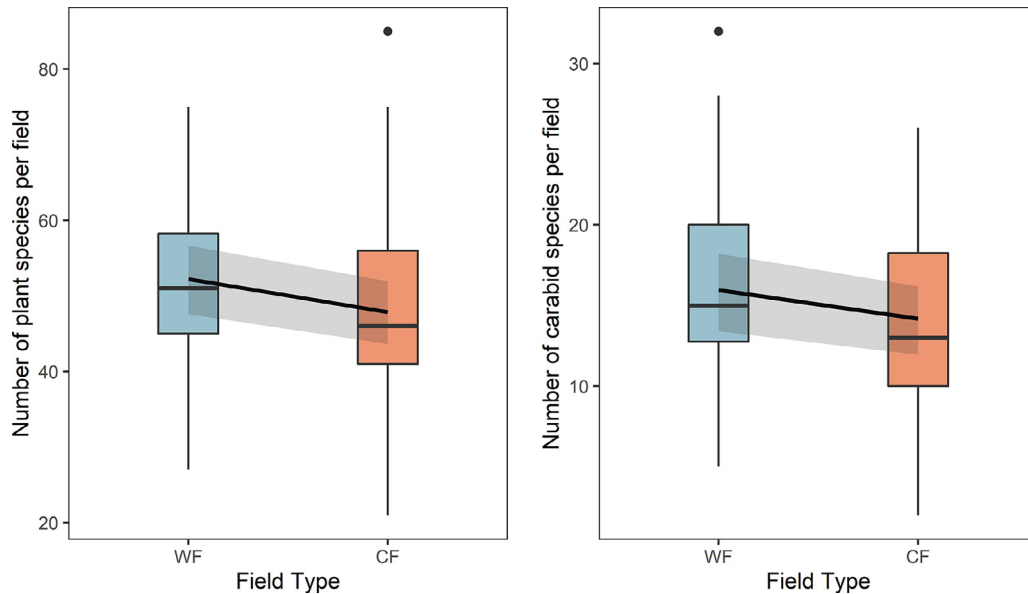
$p = 0.43$ ). Given the strong imbalance in the range of crop types across fields, we decided to omit crop type from further GLMMs. Despite the strong variations in field size and the geographical area covered by each sample region, field size and regional study area were not correlated with species richness or the proportion of species types found on each field.

For both plants and carabids, the proportion of hygrophilic species was higher on WFs on average per field (Table 1). The proportion of hygrophilic plants species (F4–5) on CFs was 38% lower than WFs (C.I.<sub>95%</sub> = 19–47%). For hygrophilic carabids, the proportion on CFs was 39% lower (C.I.<sub>95%</sub> = 21–52%). The opposite was observed, in part, with CFs having a 41% higher

proportion of xerophilic carabids on average per field than WFs (C.I.<sub>95%</sub> = 10–81%). No measurable effect of field type was observed on the presence of Red List species, semi-humid plants, or carabids surveyed in neighbouring wetland sites. All models explained very little of the overall variation in plant and carabid species richness, with marginal and condition  $R^2$  indicating that the random effect of study region far outweighed the fixed effects.

### Relationships between vascular plants and ground beetles

We observed similar trends amongst plants and carabids in regional hot spots of diversity (correlation of regional



**Fig. 4.** Number of plant (left) and carabid (right) species found on wet fields (WF) and control fields (CF). The boxplots summarize the observed species richness on each field across all regions (60 data points each). The black line represents the predicted results from the GLMMs for plant and carabid richness as a function of field type with sample region as a random effect. The grey ribbon around the lines is the 95% confidence interval for the fixed effect field type.

species richness between the two groups, Pearson's  $r = 0.58$ ). Despite the correlation among regional species diversity, correlation was low at the field level (Pearson's  $r = 0.20$ ) and the number of plant species was a poor predictor for carabid species when added as a fixed effect to the GLMM. However, the proportion of high humidity rating plant species (humidity rating of F4–5) on a field was associated with not only the proportion of hygrophilic carabids at the site, but also the total number of carabid species (Table 1). In the latter case, adding the proportion of humid plant species to the model as an interacting term with field type highlighted that this pattern was only seen on CFs (Table 1; Fig. 5). Reversing the log link, the number of carabids on CFs increased by 3% (C.I.<sub>95%</sub> = 0.6–5.5%) with every 1% increase in the proportion of humid plants. Alternatively, an examination of the inverse relationship revealed that the proportion of hygrophilic carabids had no relation to total plant species number.

### Plant and ground beetle assemblages

The ordination plots indicate marginal differences between plant and ground beetle assemblages found on WFs vs CFs (Fig. 6). Despite the strong overlap of the WF and CF polygons, results from the PERMANOVA analysis still indicated a significant difference for both vascular plant ( $p = 0.046$ , Table 2) and ground beetle assemblages ( $p = 0.05$ , Table 2). Carabid assemblages found on arable land versus those found in nearby wetlands were decidedly distinct ( $p = 0.001$ , Table 2). The ordination plots for each species group on WFs and CFs show no obvious pattern in

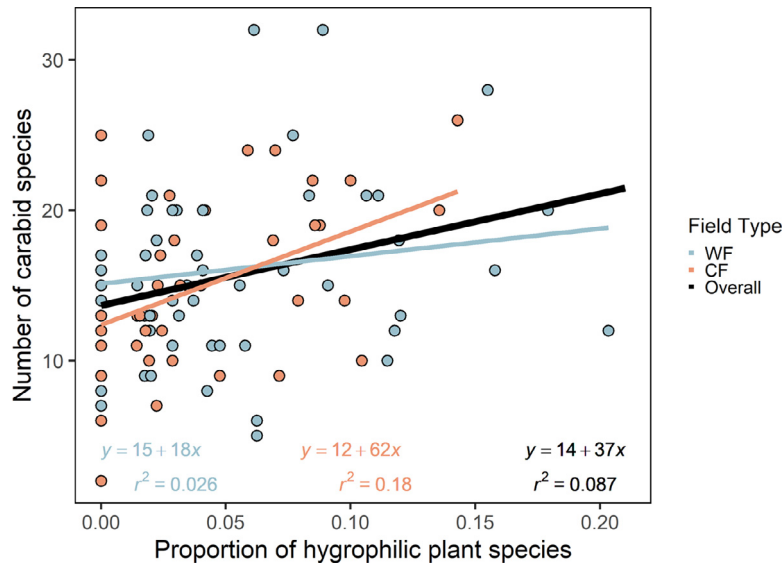
the spread of species according to humidity rating, though in the case of carabids, xerophilic species tend more towards the right side of the graph occupied by the CF polygon. Alternatively, there is clear separation between the carabids found on arable land and those in wetlands (Fig. 6B). The green polygon representing the wetland sites is dominated by blue, hygrophilic species, whereas most other species primarily occur within or near the polygons belonging to arable land.

The indicator species analysis supported earlier findings, highlighting that WFs were distinct from CFs and do seemingly support more hygrophilic species. Nonetheless, few priority threatened species were associated with WFs (see Appendix A: Table 4). The humidity ratings for the indicator species followed a rough gradient with indicators of CFs and arable land mostly comprised of xero-mesophilic species, WFs of meso-hygrophilic species, and wetlands of hygro-stenohygrophilic species. 12 of the 13 RL-species with an indicator status for carabids belonged to the wetland sites. Notably, *Drypta dentata* (4) was an indicator for WFs. Most often found in flood plains, this species is also not uncommon to extensively-managed agricultural land (Freude et al., 2004). For carabids, indicator species of arable land as a whole were mostly common mesophilic species typical of open cultural land. The same was true for the indicator species of vascular plants.

### Landscape effects on diversity

The best model describing the effect of the surrounding landscape on vascular plant species richness included the

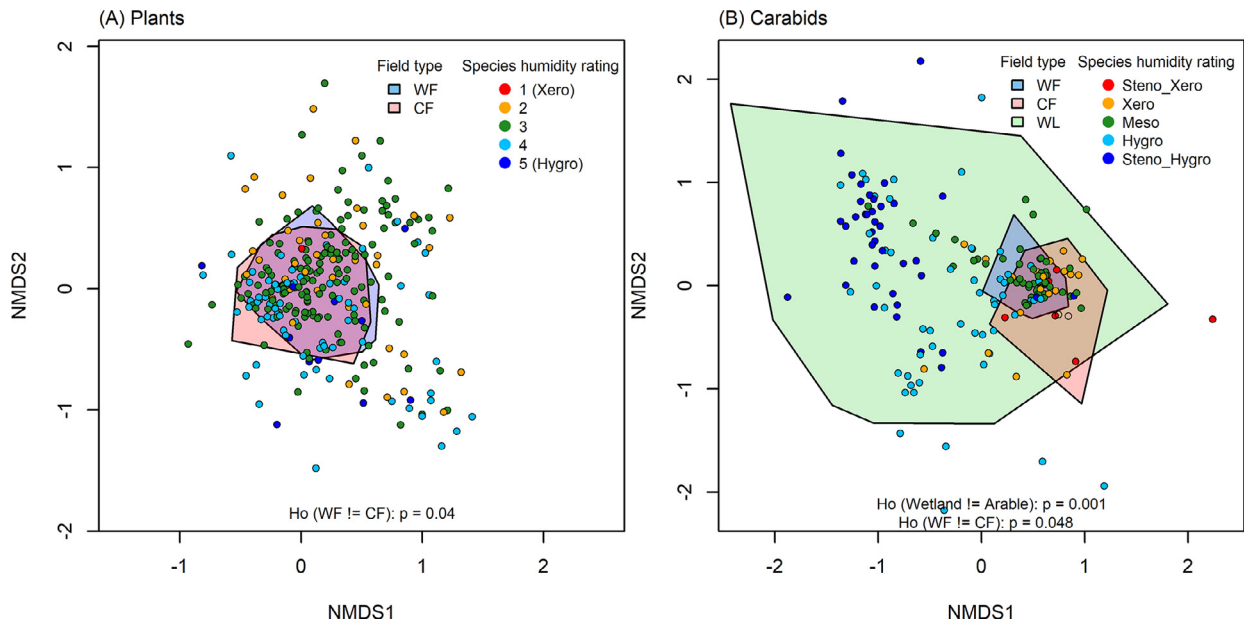




**Fig. 5.** Proportion of hygrophilic plant species plotted against the number of carabid species. Trendlines for the relationship are plotted for all fields (black), control fields (red) and wet fields (blue). The line equations and  $R^2$  are indicated at the bottom of the plot.

variables field type, distance to standing water and the proportions of roads, standing water, and forest within the 50 m buffer (Appendix A: Table 5A). Nakagawa’s marginal and conditional  $R^2$  for the model were 0.23 and 0.40, respectively, indicating that the landscape features explained a reasonable amount of the variation in plant numbers after accounting for region. Vascular plant species richness was found to significantly increase with the proportion of standing water (estimate after reversing the log-link: 1.2 times

more plant species per 10% increase in the amount of standing water within 50 m, C.I.<sub>95%</sub> = 1.01–1.43) and roads (1.12, C.I.<sub>95%</sub> = 1.04–1.22) around the field. Species number also decreased with increasing distance from standing water (0.98 plant species per 100 m, C.I.<sub>95%</sub> = 0.96–0.99). No landscape metrics had a detectable effect on carabid species richness (Appendix A: Table 5B). The best model included only field type and the proportion of the 50 m field buffer made up of hedge features. Marginal and conditional



**Fig. 6.** Ordination plots comparing (A) plant and (B) carabid community assemblages found at the sample sites. Each point represents a species and the vertices of the blue (wet fields, WFs), red (control fields, CFs), and green (wetlands, WL) polygons represent the assemblages observed at each site, generated and plotted on a nonparametric multidimensional scale using the R package ‘vegan’. Results of the PERMANOVA test of the effect of field type on community are displayed at the bottom of each plot. The humidity rating of each species is displayed according to point colour, with red representing xerophilic species and blue hygrophilic.

**Table 2.** PERMANOVA results for the effect of field type, crop type, and sample region on plant and carabid assemblages on wet fields (WFs), control fields (CFs), and, for carabids, in nearby wetland sites (WL).

	Source	df	SS	MS	F	R <sup>2</sup>	p
WF vs CF (plants)	FieldType	1	0.31	0.31	1.45	0.01	0.046*
	Region	9	3.76	0.42	1.94	0.13	0.001***
	CropType	8	4.03	0.50	2.34	0.14	0.001***
	Residuals	101	21.73	0.22	0.73		
	Total	119	29.84				
WF vs CF (carabids)	FieldType	1	0.38	0.38	1.48	0.01	0.050*
	Region	9	3.96	0.44	1.70	0.12	0.001***
	CropType	8	3.25	0.41	1.57	0.10	0.001***
	Residuals	101	26.22	0.26	0.78		
	Total	119	33.82				
Wetlands vs Fields (carabids)	WL/Arable	1	10.62	10.62	33.07	0.13	0.001***
	Region	9	8.52	0.95	2.95	0.10	0.001***
	Residuals	202	64.85	0.32	0.77		
	Total	212	83.99				

df: degrees of freedom SS: Sum of Squares, MS: mean of squares; F: F-statistic; R<sup>2</sup>: coefficient of determination.

\*:  $p < 0.05$ , \*\*:  $p < 0.01$ .

\*\*\*:  $p < 0.001$ .

R<sup>2</sup> were 0.04 and 0.35, indicating that study region, as a random effect, was responsible for capturing most of the variation in species number. Field type (WF/CF) remained an important factor determining plant and carabid species richness in all models.

## Discussion

Even though agricultural intensity was high in all ten regions and most fields possessed drainage systems, wet arable land was still present in the agricultural landscape and a higher proportion of hygrophilic species could be observed on WFs. The potential for the colonization or also the promotion of rare temporary wetland species therefore exists. Despite this, WAL under current use does not appear to serve as habitat for these target species. Very few rare species of the *Nanocyperion* and *Bidention* plant communities associated with temporary wetlands were observed in this survey. Likewise, the vast majority of surveyed carabids on the sample fields were species common to intensively managed cropland and target wetland species were rare.

### Increased plant and carabid species richness on wet fields

The higher numbers of plant and carabid species observed on WFs compared to CFs suggest that the periodic episodes of standing water on WFs causes a more heterogeneous habitat. Since the fields are in most cases only partially affected by waterlogging, different habitat types emerge on the same field. The same effects were observed by

Lukács et al. (2013) on temporarily waterlogged fields in Hungary, although in that case more endangered species were also observed. Seidl, González, Kadlec, Saska and Knapp (2020) studied carabid diversity on fields partially affected by defective sites where crops failed to grow due to sowing failures, extreme soil humidity, or missing nutrients (field defects). While fewer carabid species were observed on the defective sites compared to areas with complete crop cover, a few indicator species unique to these sites were also observed and these increased overall species richness per field (Seidl et al., 2020). Brose (2001) found that the richness of vascular plant species increased with longer periods of water logging on arable fields in Germany. Likewise, the abundance of habitat-specific carabid species increased with the density and mean duration of waterlogging (Brose, 2003b).

Despite higher local species richness on WFs, the size of the regional species pools of either field type was identical and average carabid beta diversity across regions was higher for CFs. This implies that variability in the species observed on CFs was higher than WFs. The community ordination plots also support this, with CFs having a larger polygon. This may in part be explained by the high species turnover across crop types outweighing the effect of field type on species assemblages, as seen in our PERMANOVA results. On the other hand, most fields identified as CFs also occurred within high potential regions of the wetness potential map. While all of the CFs had sufficient drainage to avoid large-scale flooding in our winter visits, fine-scale drainage issues in corners and margins were detectable during the sampling of some CFs. Wet microhabitats on our CFs may have been sufficient to support some hygrophilic species more strongly associated with WFs. This is supported by the fact that the relationship between hygrophilic plant species and carabid

species totals is only seen on CFs, i.e., CFs with high hygrophilic plant ratios and carabid species totals were probably more akin to WFs. Here, the consideration of number of individuals / percent cover of each species would have elucidated potential differences between species assemblages on CFs/WFs; by only considering species presence, rare occurrences could not be distinguished from common ones.

The large differences in species numbers across regions may be explained by multiple factors. Biodiversity on arable land is strongly affected by crop culture (Patterson, Sanderson, & Eyre, 2019; Sirami et al., 2019). Though our models did not detect a strong effect of crop type on species richness, this may be due to the moderate correlation between region and crop type as well as the imbalance in crop type among our surveyed fields. Crop type played a significant role in structuring the assemblages of plants and carabids on our fields and we expected that this would be reflected in species numbers as the crops themselves and their respective management affect the surrounding environment in varying ways (Gerhards, Dieterich & Schumacher, 2013). The arable weed diversity in maize fields, e.g., is often low due to the late sowing date, intensive use of herbicides at early growth stages, and high light competition at later growth stages (Gerhards et al., 2013). Additionally, many of the local factors that dictate crop choice, including climate, soil type, differences in management, and landscape diversity, would also impact species presence. The species pools of surrounding structure-rich habitats such as field margins, hedge rows, and wetlands are known to affect species composition on arable land (Martin et al., 2019; Purtauf et al., 2005; Weibull, Östman & Granqvist, 2003) and, at least for plants, our landscape analysis supports this to some degree. The large nature conservation area in the Neeracherried region, for instance, may explain the relatively high species numbers compared to other northern regions. Alternatively, the enhanced soil temperatures of the Orbe valley's dark, organic soils would also affect species composition.

### Deficit of rare and threatened character species

The communities of arable weed species found at the margins of WFs and CFs were similar to observations made in Baden-Württemberg in 2011 (Gerhards et al., 2013): few generalist species were observed on nearly all fields and characteristic arable weed species were rare. These findings also agree with the general trend of decreasing arable weed species diversity in Switzerland over the last century (Richner, Holderegger, Linder & Walter, 2017). The reasons can be manifold. Intensive agriculture utilizing fertilizers and pesticides is probably one important reason for the absence of target plant species (Geiger et al., 2010). Additionally, the waterlogged period may have been too short or infrequent for specific wetland species to develop on some of the sites (Brose, 2001). Further, the establishment of these species requires their presence in the soil seedbanks. These

fields were drained several decades ago or more, and WAL now only occurs due to deteriorated drainage installations. The seedbanks of former wetland plants may no longer be able to germinate, even though under some conditions wetland plants can reestablish following 50–150 years of drained conditions (Alderton et al., 2017). In this case, reestablishing populations of rare arable weed species of the *Nanocyperion* and *Bidention* plant societies on WAL may require targeted reintroductions by sowing seeds harvested from remnant populations in local wetlands (Albrecht, Cambecèdes, Lang & Wagner, 2016).

The high percentage of threatened carabid species found in nearby wetlands versus on the fields highlights the importance of perennially available, diverse and structure-rich wet habitat for their occurrence. In this study, however, not even the vicinity to more natural, structure-rich habitats had a discernable effect on the number of carabid species on arable land. While other studies have shared similar results (Brose, 2003b; Fusser et al., 2018), Martin et al. (2019) synthesis of the effects of landscape on biodiversity in agroecosystems suggests that the effects of semi-natural habitat are nonlinear, and weakest at the moderate proportions seen in landscapes like our sample regions. They hypothesize that small increases in semi-natural habitat in these landscapes may only serve to dilute populations until a critical threshold is reached and positive effects are seen in neighbouring arable land (Martin et al., 2019). Alternatively, soil disturbances from annual ploughing, ridging, and tilling on arable land are known to reduce carabid abundance, and disproportionately target larger, less mobile species (Patterson et al., 2019). Brose (2003a) found that land use intensity, over size, isolation, and flooding duration, was the most important determinant of carabid assemblage composition in temporary wetlands. Carabid assemblages on WAL under contemporary management practices are dominated by mobile, early successional species, while isolation and disturbance from intensive land use likely prevent poor dispersers from establishing (Brose, 2003a). It is possible that many of the species of conservation interest absent from our fields fall into this latter group. Their promotion would require extensive land use coupled with a more established wet habitat network within the vicinity acting as source habitat.

### Future prospectives for wet arable land

The development and promotion of alternative land-use practices that embrace WAL are required to support priority wetland species on arable land. While agricultural production on conventional fields with intact drainage systems is clearly enhanced, the variable effects of drainage systems on the water balance, nutrient and pesticide transport, greenhouse gas emissions, as well as wetland habitat availability, call to question the long-term sustainability of ubiquitous

drainage efforts (Gramlich et al., 2018). Where site-specific factors cause high cumulative risks to the environment with relatively little economic gain, accepting and working with WAL may be the logical management decision (Gramlich et al., 2018). One solution may be the cultivation of high-humidity tolerant crops, eliminating the need for a tradeoff between production and biodiversity promotion (Verhoeven & Setter, 2010). First attempts towards establishing a paddy-rice cultivation technique that promotes biodiversity have been made by Agroscope, Switzerland, where pilot experiments from 2017–2019 show the potential for rice cultivation north of the Alps (Jacot, Churko, Burri & Walter, 2018). A further option would be the inclusion of WAL with extensive management as a new type of financially supported biodiversity promotion area in Switzerland (FOAG, 2019).

For successful reestablishment and to maximize benefits to wetland biodiversity, rewetting initiatives should prioritize locations where WAL could supplement and bolster the existing wetland network (Churko, Walter, Szerencsits & Gramlich, 2020). In this fashion, the promotion of WAL would not only add to the limited available habitat for target species of temporary wetlands, but also serve to improve connectivity between populations of a broad range of wetland species (Churko et al., 2020). Along short-range dispersal routes, WAL could improve survival rates for migrating individuals by providing refuge and resources (Taylor, Fahrig, Henein & Merriam, 1993). WAL could also act as a stepping stone habitat to open up migration routes between isolated populations, improving genetic exchange and allowing climate-driven range shifts (Lawler, Ruesch, Older, & McRae, 2013; Rayfield, Pelletier, Dumitru, Cardille, & Gonzalez, 2015; Saura, Bodin, & Fortin, 2014).

## Conclusion

Widespread drainage installations have reduced the prevalence of temporary wetlands in the agricultural landscape while simultaneously diminishing connectivity within the wetland network. Our results indicate that even locations where drainage is absent or deteriorated provide inadequate habitat for target temporary wetland species. Very few habitat-typical and endangered vascular plant and ground beetle species were found on WAL in Switzerland in the present survey. Since wet fields still host significantly more hygrophilic species than control fields, the potential for the promotion of species with more restrictive habitat requirements is suggested. In locations where site-specific trade-offs favour the promotion of WAL, target temporary wetland species would benefit from a move to more extensive management, the cultivation of humidity tolerant crops, and/or an improved network with surrounding wetlands.

## Declaration of Competing Interest

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

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2021.03.004.

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