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# Responses of rice paddy dragonflies to fertilisation in a mesocosm experiment

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ABSTRACT

Freshwater biodiversity has been decreasing globally, with wetland habitats facing significant loss due to climate change and changes in land use. In Switzerland, over 90 % of low-elevation wetland habitats have been lost since 1850, mainly due to land transformation for agriculture. Recently, farmers started cultivating paddy rice in Switzerland to meet the increasing food demand and to support wetland biodiversity, particularly dragonflies. However, rice is often produced at high fertiliser levels, raising concerns about potentially harmful effects of high nutrient levels on dragonflies developing in rice paddies. Here, we assessed the impacts of nitrogen fertilisers on dragonflies from a conservation perspective. We exposed three dragonfly species to mineral and organic fertilisers at different concentrations in experimental mesocosms mimicking rice paddies. The effects of fertilisation on survival as well as development time and size at emergence were quantified. In total, 77 % of all dragonfly larvae survived until emergence, and survival was not significantly affected by either fertiliser type at concentrations that are used in Swiss rice paddies (ranging from 25 kg N/ha to 150 kg N/ha). Also, there were no negative impacts of any fertiliser type and concentration on emergence time and body size, which albeit differed significantly among the three dragonfly species. The study thus provides valuable and encouraging insights for conservation and management strategies aimed at promoting wetland biodiversity, particularly the diverse and vulnerable dragonflies, through paddy rice cultivation.

## 1. Introduction

There has been a significant decrease in freshwater biodiversity worldwide, and unfortunately, this trend is not slowing down (Dudgeon and Strayer, 2024). The main reason for this decline is the global loss of 21 % of wetland habitats due to changes in land use (IPBES, 2019, Fluet-Chouinard, Stocker, Zhang et al., 2023). In Switzerland, the situation is even more alarming because more than 90 % of wetlands in the lowlands have been lost since 1850, with the main culprit being land transformation for agricultural purposes (Gimmi, Lachat, Bürgi, 2011). There continues to be a tension between agricultural production and the preservation of biodiversity which is exacerbated by climate change. To mitigate this problem, more attention needs to be paid to crops that can thrive in warmer conditions to meet the growing demand for food. Ideally, such crops would also provide habitats for biodiversity. In Switzerland north of the Alps, the cultivation of paddy rice, an exotic crop for this region that grows increasingly well due to warming temperatures, may be a land-sharing approach that combines agricultural production and biodiversity conservation. Cultivating paddy rice fields creates new aquatic habitats in a landscape dominated by arable fields and pastures, providing an example of combining biodiversity conservation and food production (Kremen, 2015, Grass et al., 2020). Rice paddies can support wetland biodiversity and could be used for wetland species conservation efforts.

Dragonfly surveys conducted in Swiss rice paddies revealed a high diversity and abundance of these insects (Jacot et al., 2018; Gramlich et al., 2020, Monnerat et al., 2021). Among them are pioneer species, which are adapted to changes in water levels throughout the year, such

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as the red-listed dragonfly species *Sympetrum depressiusculum* (Red List status vulnerable) or *Orthetrum albistylum* (near threatened; Jacot et al., 2018; Gramlich et al., 2020, Monnerat et al., 2021). Rice paddies, which are periodically drained, act as temporary water bodies, which are an important habitat for many aquatic species (Wellborn et al., 1996). Research suggests that the presence of the dragonfly species *S. depressiusculum* may be limited by unsuitable abiotic conditions rather than other reasons, like for example predation (Šigutová et al., 2018).

Rice cultivation requires substantial nutrients for optimal growth and yield. Fertiliser may lead to high nitrogen concentrations in the water which may be detrimental to many aquatic organisms (Camargo and Alonso, 2006). However, the nitrogen concentrations that could negatively impact dragonflies, particularly their aquatic larvae, remain largely unknown. This raises questions about the potential effects of high nutrient loads on the development and fitness of dragonflies in Swiss rice paddies. It is crucial to assess whether exposing animals to nitrogen fertilisers poses any potential harm, particularly when these animals are a focus of conservation efforts (i.e., land sharing). The creation of attractive breeding habitats that attract dragonflies early in the season and expose them to fertiliser could potentially create an ecological trap (Melendez et al., 2022, Gameiro et al., 2024). In addition to the potential effects of fertilisation on the survival of dragonflies, it is also important to consider more subtle effects on individual traits, such as development time and size at emergence. In various taxonomic groups with complex life cycles, there is evidence that environmental conditions experienced at the larval stage have fitness consequences that persist into the post-metamorphic stage (De Block and Stoks, 2005). In the case of dragonflies, a larger body may positively affect mating success and survival (Tsubaki and Ono, 1987, Ancco Valdivia et al., 2020).

To test if the fertilisation of paddy rice has effects on dragonfly larvae developing in these fields, we conducted an mesocosm experiment. Our aim was to investigate how management practices, particularly the application of nitrous fertilisers, can potentially affect aquatic dragonfly larvae. There may be effects on fitness parameters, such as survival of the larvae, body size and the timing of emergence. We hypothesised that higher nitrogen concentration will be reflected in lower survival of the larvae, extended time of developmental and decrease in body size. A decrease in fitness-related life history traits would indicate that fertilisation has negative effects and that there may be conflict between biodiversity promotion and yield in rice paddies. Our study is the first to experimentally investigate the effect of rice paddy fertilisation on dragonflies, an iconic indicator of wetland biodiversity. The results can help to define a land-sharing strategy where both agricultural production and biodiversity promotion are achievable.

## 2. Material and methods

### 2.1. Study organisms

The focus of our study was on the skimmer dragonflies - *Sympetrum sp.*, which are found in high abundances in Swiss rice paddies (Gramlich et al., 2020, Monnerat et al., 2021). On June 20th, 2023, we captured *Sympetrum sp.* dragonfly larvae from a conventionally used rice paddy in Western Switzerland. Using a kick net we collected a total of 320 larvae, with 96 individuals measuring approx. 17 mm and identified as *Sympetrum depressiusculum*, 96 individuals of the same length identified as *Sympetrum sp.* (suspected *S. striolatum* or *S. vulgatum)*, and 128 smaller individuals measuring approx. 15 mm, also identified as *Sympetrum sp.* The challenge in clearly distinguishing between *S. striolatum* and *S. vulgatum* larvae is due to underdeveloped species identification characteristics prior to metamorphosis (Küry, 2020, Wildermuth, Martens, 2018). The identification to species level of *S. striolatum* and *vulgatum* was therefore performed on adult individuals upon emergence and from the shedded exuviae. To prevent intraguild predation (Yang and Rudolf, 2010; Rudolf, 2019) between smaller and larger larvae in the mesocosms, we divided the larvae based on their size across the five blocks. This resulted in 3 blocks with tanks containing 4 large *S. depressiusculum* and 4 large *Sympetrum sp.*, and 2 blocks with tanks containing 8 small *Sympetrum sp.* To maintain statistical power and avoid overfitting, we pooled size categories across treatments and species due to limited replication within each group. While the size category was evaluated in separate models and showed some influence on survival and emergence time, the magnitude of these effects was small and unlikely to be meaningful in real-world context. Therefore, size was excluded from the final models to allow a clearer focus on species specific responses of the core treatments.

### 2.2. Paddy rice production in Switzerland

Paddy rice has been cultivated in Switzerland since 2017. The cultivation process begins mid-May when farmers level the field and flood the paddies to a depth of about 10 cm, using water pumps. The rice typically range from 0.4 to 1 hectare in size and yield an average of 2.5–8 tons raw rice per hectare. There is no mid-season drainage. Farmers transplant seedlings, taking advantage of early-season flooding to suppress weeds and promote biodiversity. The use of pesticides in these paddies is prohibited by Swiss law (The Swiss Federal Council, 1998). The recommended fertilisation standard for nitrogen in rice cultures is 110 kg N/ha (Sinaj et al., 2017), but fertiliser application is often limited to an average of 30–50 kg N/ha in paddy rice. Harvest occurs between September and October, completing the season cycle.

### 2.3. Mesocosm experiment

We conducted a factorial mesocosm experiment to determine whether nitrous fertiliser affects the development of *Sympetrum* sp. dragonflies. We exposed a total of 320 larvae to two fertilisers most commonly used in rice paddies in Switzerland. The mineral fertiliser (prilled Urea 46 % N, Hauert) and the organic fertiliser (Biorga Quick, 12 % N and 80 % plant derived organic substances, Hauert), both commercially available, were tested across a gradient of four concentrations of nitrogen (0, 25, 75 and 150 kg N/ha). The concentrations reflect the amounts of fertilisers used in Swiss rice paddies. To prepare the mesocosms (Fig. 1), we first grew rice plants two weeks prior to the start of the experiment. The 2-week-old plants (approx. 10 cm tall) were transplanted into the mesocosms. The mesocosms were 80 L tanks (0.28 m) filled with a 10 cm layer of sieved (5 mm mesh sieve) soil from the Agroscope's experimental sites. Soil was not treated with

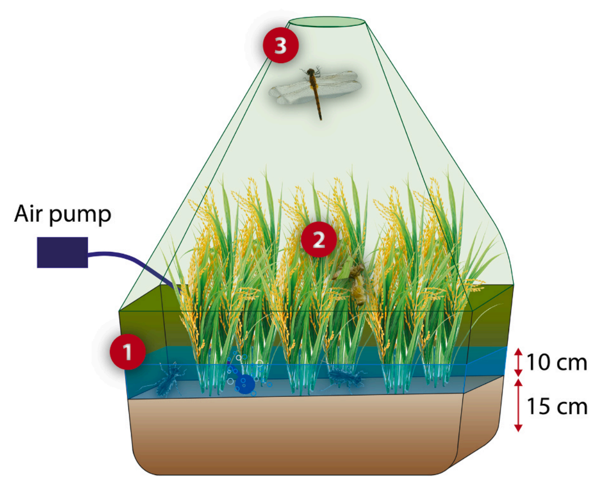


**Fig. 1.** Mesocosm set up with rice plants and dragonflies in different developmental stages: 1) larvae, 2) metamorphosing individuals, 3) fully emerged adult dragonfly. The substrate height was: 15 cm and water depth kept at 10 cm. The rice plants were 2 weeks old and around 10 cm tall upon transplantation.

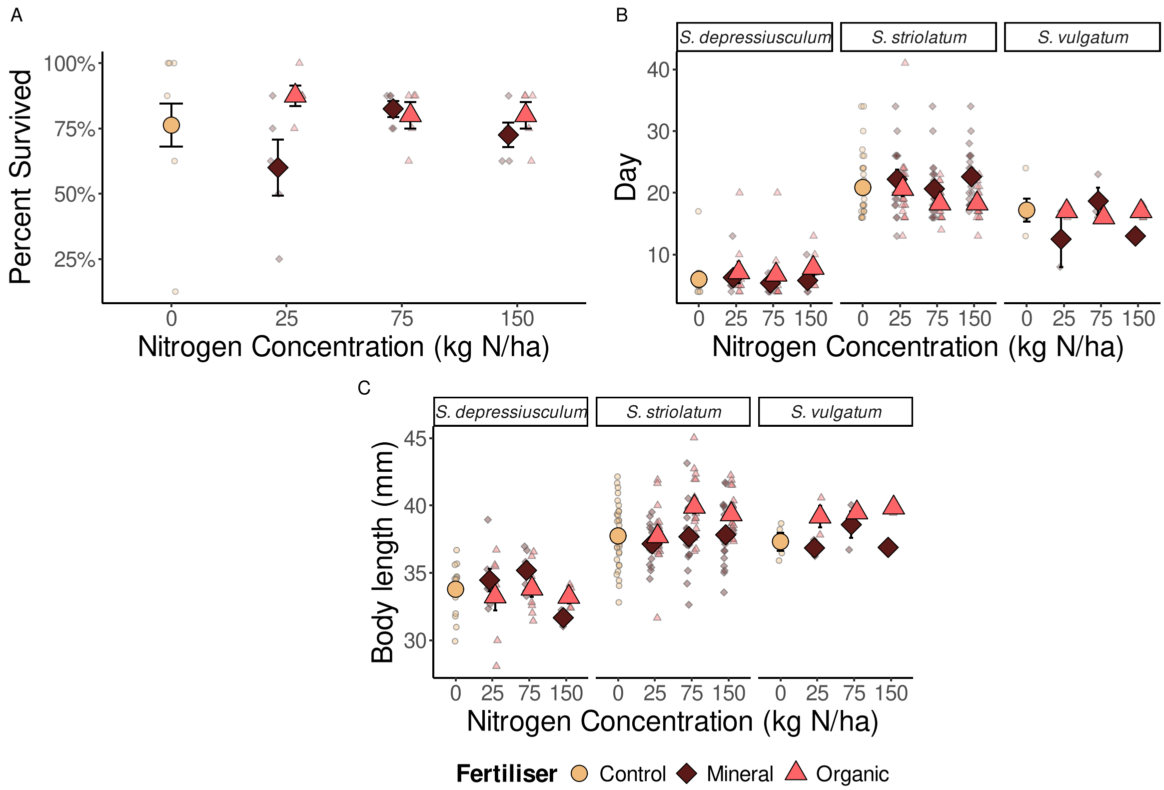


**Fig. 2.** A. Survival of dragonflies, B. Developmental time of dragonfly and C. Body length in control treatment (yellow circles) and exposed to organic (red triangles) & mineral fertiliser (brown squares), at nitrogen concentrations of 0, 25, 75, 150 kg N/ha. Large shapes represent means with SE, while small shapes represent the individual measurements.

agrochemicals and is representative of the mineral soil type of Swiss paddy rice fields. The mesocosms containing transplanted rice plants were filled with tap water up to a depth of 10 cm from the substrate surface (Fig. 1). To account for water loss from evaporation, we adjusted the water level 1–2 times per week based on temperature and evaporation rate. A low-intensity air pump was used in each tank to simulate oxygen inflow typical of Swiss rice paddies, where daily water pumping occurs. Pumping intensity was equal across treatments, and measured dissolved oxygen (DO) levels (around 7 mg/L at the start of experiment, Fig. 3D) aligned well with field observations (Supplement 2, Fig. A1; Mowjood and Kasubuchi; 1998). The mesocosms were covered with a 1 cm mesh net to prevent emerged dragonflies from escaping.

Our design resulted in 2 × 4 factorial combinations, each replicated five times. The replicates were arranged into five spatial blocks. Treatments were assigned randomly to mesocosms within blocks. We applied fertiliser once at the beginning of the experiment, 2 days before releasing the dragonfly larvae into the mesocosms. Between the day of metamorphosis of the first dragonfly in late June and early August 2023, we recorded the emergence day and measured the body size of newly metamorphosed dragonflies. To do this, we placed the dragonflies in a petri dish and took images from above, using a millimetre scale for reference. The body size was measured from head to tail using digital images analysed with Fiji (Schindelin et al., 2012). Survival rates were estimated at the end of the experiment based on the number of metamorphosed individuals. Mesocosms were checked twice a day. We also measured water quality and chemistry, which we describe in more detail below.

The dragonfly larvae were kept in the greenhouse at a temperature of 27.5°C until the beginning of the experiment. They were fed ad libitum with a homogenous mixture of *Daphnia magna, Chaoborus sp.* and *Tubifex sp.* (200 ml in total) once per week as food for the dragonfly larvae.

The experiment was conducted under semi-natural conditions in a greenhouse with an automated roof that closed during rain or strong wind. The experiment started on 24th of June 2023, and was finished at the beginning of August, with a running time of 40 days.

### 2.4. Water quality

The water chemistry and abiotic parameters were monitored during the initial two weeks of the experiment thrice per week and then twice per week. The water chemistry was assessed for $NO_2$-N (nitrite nitrogen, further referred also as nitrite) and $PO_4$ (ortho-phosphate), measured during the sampling process using a portable parallel analyser (HACH SL1000) and ChemKeys. The detection range of the ChemKesy for $NO_2$-N and $PO_4$ was within 0.003–0.690 mg/L and 0.20–5.00 mg/L, respectively. Additionally, abiotic parameters such as dissolved oxygen, water temperature, conductivity, and pH were measured with a multiparameter device (HACH HQ4300 with PHC10101, CDC40101, LDO10101 probes).

### 2.5. Plant biomass

The dry plant biomass was measured 46 days after the experiment started and after the emergence of all surviving dragonfly larvae. Ten haphazardly selected rice straws were taken from each tank and dried for 36 h at 80°C. The dried rice plants were weighted with a precision balance in grams. Biomass was recorded to document the effect of different fertilisation regimes on plant growth.

### 2.6. Data analysis

Statistical analyses were conducted using R (version: 4.3.3., R Core Team; 2023) and the lme4 package (Bates et al., 2015). Survival of dragonfly larvae (proportion of individuals emerging as adults per mesocosm) was analysed using a generalised linear mixed model (GLMM) with binomial errors, testing for the effects of fertiliser type,

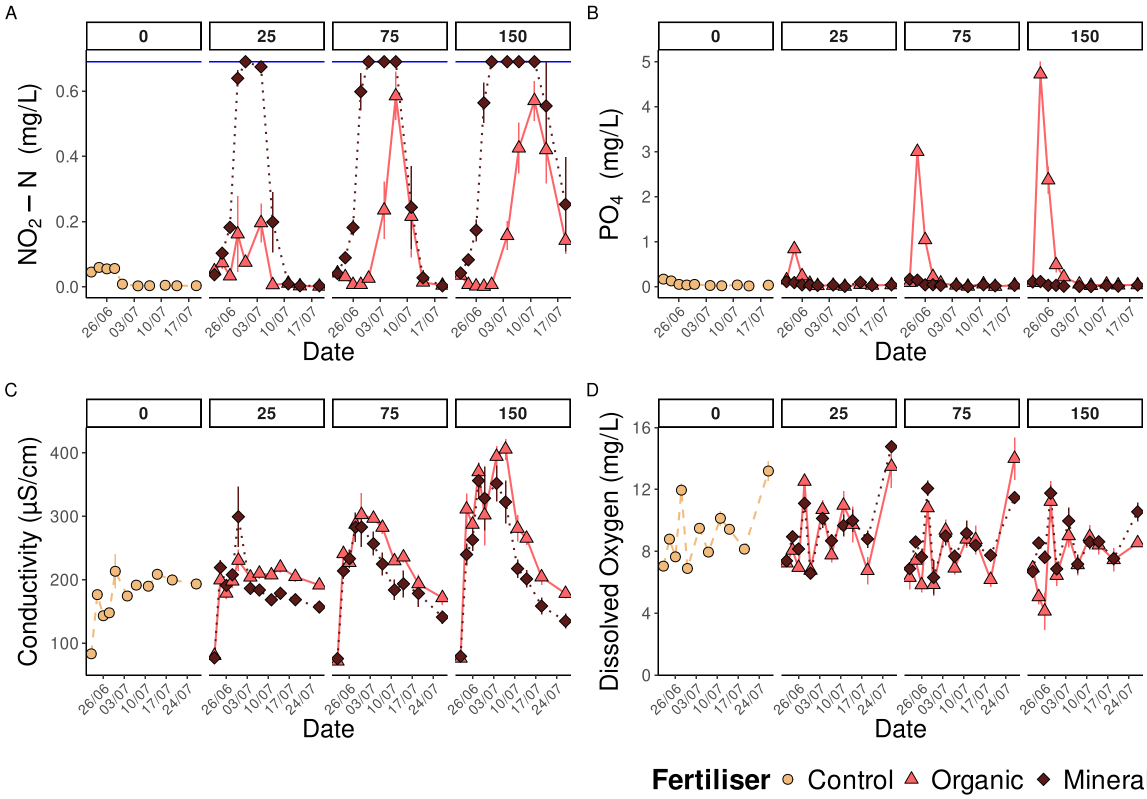


**Fig. 3.** Measurements of water quality parameters. A. Nitrate Nitrogen (NO2-N) concentrations. Black horizontal bar marks the measurement limit of the device, B. ortho-Phosphate (PO4), C. Conductivity and D. Dissolved oxygen. control treatment (yellow circles) and exposed to organic (red triangles) & mineral fertiliser (brown squares). Top labels indicate fertiliser concentrations corresponding to field applications at nitrogen concentrations of 0, 25, 75, 150 kg N/ha. Blue, horizontal line in A. indicates the detection limit of the device.

concentration and their interaction. Block was included as a random effect. Time to emergence and size (adult length) of dragonflies were analysed using linear mixed models testing for the effects of fertiliser type, fertiliser concentration and species, as well as their interactions. Mesocosms and blocks were included as random effects to account for the non-independence of dragonflies emerging from the same tanks. The lmerTest library was used for significance tests of fixed effects (Kuznetsova et al., 2017), applying type III sums of squares and Satterthwaite's approximation for degrees of freedom for all models, except survival. For the binomial distributed survival data we estimated type III sum of squares and used the Wald $\chi^2$ approximation for degrees of freedom with the car library (Fox and Weisberg; 2019). The water quality measurements, such as conductivity, dissolved oxygen, nitrite and ortho-Phosphate concentrations were square-root transformed before analysis with a linear model, testing for the effects of fertiliser type, concentration and different timepoints. Mesocosm was included as a random effect. The water quality models were validated with an ANOVA test, using type III sums of squares and Satterthwaite's method. Plant biomass was tested for the effects of fertiliser type, concentration and their interaction using a linear model.

## 3. Results

### 3.1. *Dragonflies*

#### 3.1.1. *Survival*

In total, 77 % (CI: 43 %-98 %) of all dragonfly larvae survived until emergence in our experiment. There was considerable variation in survival among mesocosms due to isolated replicates producing very few adult dragonflies, but overall survival was similar across treatments (Fig. 2A). Accordingly, neither the fertiliser type (Wald's $\chi^2 = 1.74$, df = 1, $P = 0.187$) nor the concentration (Wald's $\chi^2 = 3.74$, df = 3, $P = 0.291$) had a significant effect on survival. However, there was a significant interaction between fertiliser type and concentration (Wald's $\chi^2 = 8.97$, df = 3, $P = 0.030$), which reflects the low average survival at 25 kg N/ha concentration with mineral fertiliser, that mainly came about by one mesocosm showing very low survival (25 %) for unknown reasons (Fig. 2A). There was also one mesocosm in the control treatment where survivorship was very low (Fig. 2A).

#### 3.1.2. *Emergence time*

The three dragonfly species included in the experiment differed significantly in their time to emergence (Fig. 2B, Table 1). Especially the early breeding *S. depressiusculum* (Küry, 2020, Wildermuth, Martens, 2018) consistently emerged before the other two species. There were no significant main effects of fertiliser type and concentration on time to emergence, but there was a significant interaction between dragonfly species and fertiliser type (Table 1), likely reflecting that the organic fertiliser tended to speed up development somewhat in *S. striolatum* but not in the other species (Fig. 2B). None of the other interactions in the model were statistically significant (Table 1).

#### 3.1.3. *Body length*

The three species of dragonflies showed significant differences in body length (Table 1). *S. depressiusculum* was the smallest, with an marginal mean size of 33.4 mm (95 % CI: 32.7–34.1 mm), while *S. striolatum* and *S. vulgatum* had comparable sizes of 38.2 mm (37.6–38.8 mm) and 38.0 mm (36.9–39.2 mm), respectively (Fig. 2C). There was a significant main effect of fertiliser type on dragonfly body length as well as a significant three-way interaction between fertiliser type, concentration and dragonfly species (Table 1). This resulted from *S. striolatum* and *S. vulgatum* growing larger in the organic fertiliser

**Table 1**
Results of linear mixed models testing for the effects of dragonfly species, fertiliser type and fertiliser concentrations as well as their interactions on the time to emergence and the body length of successfully emerging dragonflies. Mesocosm and block were included as a random effect in both models. P-values of fixed effects are based on F tests with Satterthwaite's approximation carried out with the lmerTest library in R.

| *Response variable* | *Source of variation* | *Num DF* | *Den DF* | *MS* | *F-value* | *P-value* |
|---|---|---|---|---|---|---|
| Day of Emergence: | Species | 2 | 216.44 | 2205.93 | 198.42 | < 0.001 |
| | Fertiliser type | 1 | 57.77 | 0.01 | 0.00 | 0.974 |
| | Fertiliser concentration | 3 | 57.37 | 3.07 | 0.28 | 0.842 |
| | Species **x** Fertiliser type | 2 | 196.95 | 45.14 | 4.06 | 0.019 |
| | Species **x** Fertiliser concentration | 6 | 199.9 | 6.07 | 0.55 | 0.773 |
| | Fertiliser type **x** Fertiliser concentration | 3 | 56.45 | 1.07 | 0.10 | 0.962 |
| | Species **x** Fertiliser type **x** Fertiliser concentration | 6 | 195.24 | 18.64 | 1.68 | 0.129 |
| Body length: | Species | 2 | 181.44 | 387.54 | 105.17 | < 0.001 |
| | Fertiliser type | 1 | 66.42 | 15.98 | 4.34 | 0.041 |
| | Fertiliser concentration | 3 | 65.61 | 7.09 | 1.92 | 0.134 |
| | Species **x** Fertiliser type | 2 | 177.81 | 4.10 | 1.11 | 0.331 |
| | Species **x** Fertiliser concentration | 6 | 182.91 | 4.57 | 1.24 | 0.288 |
| | Fertiliser type **x** Fertiliser concentration | 3 | 65.24 | 2.43 | 0.66 | 0.580 |
| | Species **x** Fertiliser type **x** Fertiliser concentration | 6 | 179.69 | 8.72 | 2.37 | 0.032 |

treatments, especially at higher concentrations, which was not evident in *S. depressiusculum* (Fig. 2C). None of the other effects in the model were significant (Table 1). The marginal means of all three life-history traits for each treatment are provided in Supplementary Table A2, and effect sizes in Supplement 2 Table A1.

### 3.2. Water quality

The detailed analyses of water quality parameters are provided in Supplementary Table A1. Briefly, all parameters varied significantly over time with patterns largely corresponding to expectations based on treatments. Nitrite levels increased with fertiliser concentration ($F_{3,32}$= 103.08, $P < 0.001$) and, unsurprisingly, were higher for the mineral (urea) fertiliser type ($F_{1,32} = 177.63$, $P < 0.001$) containing more nitrite (Fig. 3A). Phosphorus was only contained in the organic fertiliser. Accordingly, we saw brief spikes in the ortho-phosphate concentrations after the addition of organic fertiliser only (Fig. 3B). The height of these spikes increased with fertiliser concentration ($F_{3,32} = 21.54$, $P < 0.001$), but even at the highest concentration, the ortho-phosphate concentrations dropped down to control levels within less than two weeks. Water conductivity increased with the increasing concentrations of fertiliser ($F_{3,32} = 38.98$, $P < 0.001$) and was different for the two fertiliser types ($F_{1,32} = 10.09$, $P = 0.003$, Fig. 3C). Finally, dissolved oxygen (Fig. 3D) concentrations were lower when more fertiliser was added ($F_{3,32} = 5.12$, $P = 0.005$), but most measurements remained between 6 and 12 mg/L, i.e. at very tolerable levels close to saturation.

### 3.3. Rice plant biomass

The dry mass of ten haphazardly selected rice plants at the end of the experiment was similar across treatments (Fig. 4). The effect of fertiliser type was marginally non-significant ($F_{1,32} = 3.874$, $P = 0.058$), likely reflecting the slightly higher weight of plants receiving the organic fertiliser at higher concentrations, but there was no significant effect of fertiliser concentration ($F_{3,32} = 1.624$, $P = 0.203$), nor was there a significant interaction of fertiliser type and concentration ($F_{3,32} = 1.541$, $P = 0.223$).

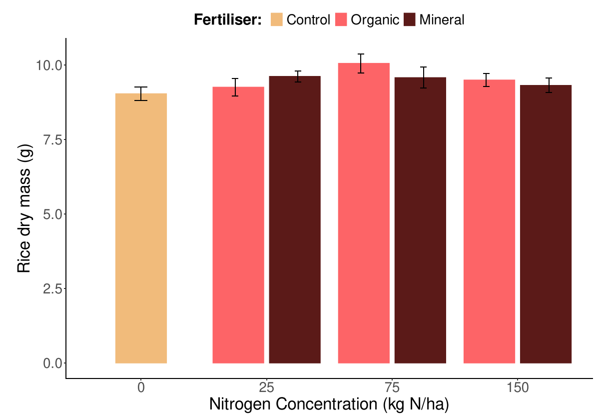

**Fig. 4.** Mean dry biomass (with SE) of 10 rice plants (without roots) at day 62 after sowing. Control treatment (yellow), organic (red), mineral fertiliser (brown), at nitrogen concentrations of 0, 25, 75, 150 kg N/ha.

## 4. Discussion

Paddy rice can serve as a substitute habitat for aquatic biodiversity, particularly for dragonflies, in landscapes that have been transformed for agricultural purposes and where wetlands were lost (Giuliano and Bogliani, 2019; Huynh et al., 2020; Monnerat et al., 2021). However, rice cultivation is characterised by its high nutrient demands, necessitating the application of fertilisers to achieve satisfactory yields (Giri et al., 2022). Because high nutrient loads can have negative effects on aquatic species and may possibly turn rice paddies into ecological traps (Melendez et al., 2022; Gameiro et al., 2024), it is necessary to understand the impact of fertilisation on species which are of conservation interest. Our experimental investigation found no negative effects of fertiliser on survival, emergence time and size of three dragonfly species (*Sympetrum* sp.) which are commonly encountered in rice paddies in Switzerland. Notably, the water quality data collected during our study demonstrated that fertiliser application did not cause possibly detrimental conditions for the dragonfly larvae. It is important to note, however, that continuous aeration in our mesocosms mitigated potential oxygen depletion from fertiliser use. In rice paddies, organic material decomposition may lead to localised hypoxic conditions, particularly in stagnant areas with limited water movement (Mowjood and Kasubuchi, 1998; Naito et al., 2014). Our setup would not have captured such effects. However field measurements of DO levels is Swiss rice paddies found values that are comparable to those observed in our mesocosms (Supplement 2, Fig. A1). This suggests that careful fertiliser management can indeed sustain both agricultural productivity and the ecological health of rice paddies, benefiting dragonfly populations.

Rice paddies are fertilised to achieve satisfactory yields. It was therefore surprising not to observe any significant differences in plant dry mass between treatment concentrations, and only near significant differences between fertiliser types. Possible explanations include the short duration of the experiment (plants were harvested before fruiting), or that the substrate we placed in the mesocosms was quite nutrient rich such that the moderate fertilisation treatments did not lead to large proportional differences among treatments. The statistical analysis of the water quality parameters showed significant changes over time and between different fertiliser concentrations and types, but these changes did not translate into significant biological effects on the dragonflies survival, emergence time or body length. This indicates that the treatments did not induce detrimental water quality conditions severe enough to affect the dragonfly larvae. The dragonfly larvae were able to thrive within the range of water quality conditions presented in this study.

In fact, we even observed weak positive effects of organic fertilisation in *S. striolatum*, which exhibited a shorter developmental period and larger body size—traits that may enhance the fitness of adult dragonflies (Tsubaki and Ono, 1987; Anholt, 1991; Ancco Valdivia et al., 2020). It is likely that organic fertilisation increased primary productivity and thus supported a richer food web in the mesocosms (Hecky and Kilham, 1988; Elser et al., 2007), enhancing food availability (or quality) for the dragonfly larvae. These findings resonate with prior studies indicating that nutrient-rich diets can promote growth in invertebrates. For instance, Orthoptera larvae fed high-phosphorus diets became larger adults (Visanuvimol and Bertram, 2011), and research on *Sogatella furcifera* showed that high nitrogen fertiliser led to faster reproduction and longer lifespans (Li et al., 2021). On the other hand, *S. depressiusculum* in our experiment metamorphosed rapidly and effects of the treatments were not observed, likely due to insufficient exposure time, while the small sample size of *S. vulgatum* limited meaningful comparison.

In conclusion, our results suggest that the application of fertiliser in these systems does not negatively impact dragonfly larvae. This is a promising outcome for the conservation of these species in rice paddies, which is further aided by the fact that Swiss law prohibits pesticide applications in water and therefore in rice paddies. While the study focused on three species from the genus *Sympetrum*, we assume that, due to their shared environment, their habitat requirements and sensitivities are comparable to other dragonfly species breeding in rice paddies. This study is one of the first to experimentally assess the effects of fertilisation on dragonfly development, and it indicates that well-managed agricultural practices can safeguard species of conservation concern in paddy rice production systems. Our research thus highlights the benefits of paddy rice for dragonflies (Giuliano and Bogliani, 2019; Huynh et al., 2020), particularly in the light of ongoing habitat loss in agricultural landscapes. Rice paddies have the potential to function as land-sharing systems, where agricultural production and biodiversity conservation can coexist successfully.

## CRediT authorship contribution statement

**Thea Bulas:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Benedikt R. Schmidt:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Formal analysis, Conceptualization. **Christoph Vorburger:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Yvonne Fabian:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

## Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used Grammarly and DeepL in order to improve language and readability. After using this tool/service, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

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## Permits

No permits were required

## People who helped

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## Declaration of Competing Interest

Yvonne Fabian reports financial support was provided by Swiss National Science Foundation. Yvonne Fabian reports financial support was provided by Ernst Gohner Foundation. Yvonne Fabian reports financial support was provided by Canton of Bern. Yvonne Fabian reports financial support was provided by Canton of Fribourg. Yvonne Fabian reports financial support was provided by Canton of Vaud. Yvonne Fabian reports financial support was provided by Canton of Valais. Yvonne Fabian reports financial support was provided by Canton Aargau. If there are other authors, they 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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None

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109823.

## Data Availability

Data will be made available on request.

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