



Do Fallow Field Biotores Function as Habitats for Aquatic Insects Similar to Rice Paddy Fields and Irrigation Ponds?

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Abstract

In Japan, abandonment of rice fields has rapidly increased, resulting in biodiversity loss. Fallow field biotores are attractive measures for compensating wetland species habitats in paddy environments. However, effective management practices of fallow field biotores for biodiversity conservation are largely unknown, especially for lentic aquatic insects (Odonata, Hemiptera, and Coleoptera). We conducted field experiments in abandoned rice terraces in western Hyogo Prefecture, central Japan. We plowed and flooded nine abandoned paddy fields and divided them into three types: paddy fields, biotores, and mixed fields. We also surveyed irrigation ponds. To assess the function of the four habitat types, we examined how species richness, abundance, and community composition of aquatic insects differed among habitat types. Aquatic insect assemblages in biotores differed from paddy fields and ponds and resembled that in a mixed field. The effects of environmental factors on the abundance and species richness of aquatic insects differ according to their order or life stages. The abundance of aquatic insects increased with surface area. The abundance of Odonata nymphs increased with water depth, whereas that of Hemiptera nymphs and Coleoptera larvae decreased. The abundance of Odonata nymphs and Hemiptera adults increased with increasing vegetation cover, whereas the species richness of aquatic insects decreased. Thus, it is important to prevent high vegetation cover by plowing and create a water depth gradient for creating habitats for multiple taxa. We suggest that creating or maintaining mosaic habitats, including paddy fields, biotores, and ponds could enhance aquatic insect diversity in abandoned rice terraces.

Keywords Aquatic true bug · Damselfly · Dragonfly · Rice-field abandonment · Rice terrace · Water beetle

要旨

日本では水田における耕作放棄地の面積が増加しており、それに伴い生物多様性が減少している。休耕田ビオトープは水田環境における湿地性生物の保全手法として着目されているが、特に止水性水生昆虫類(トンボ目・カメムシ目・コウチュウ目)の保全に有効な管理手法に関する知見は限られる。本研究では、耕作放棄田の管理手法を提言することを目的として、兵庫県西部の棚田において野外操作実験を行った。9枚の耕作放棄田を復旧し、稲作を行う水田と湛水後は野放しにした休耕田、水田の一部を休耕した中間型を準備した。周辺のため池も調査地とした。生息地としての機能を評価するため、4つの生息地タイプ間で水生昆虫類の種数、個体数、種組成を比較した。解析の結果、ビオトープの種組成は水田、ため池とは有意に異なり、中間型と類似していた。また、環境要因が水生昆虫類の種数や個体数に与える影響は目や発育ステージ(幼虫・成虫)によって異なった。水生昆虫類の個体数は、水域面積の増加に伴い増加した。トンボ目幼虫の個体数は水深が深くなるにつ

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れて増加したが、カメムシ目とコウチュウ目の幼虫の個体数は減少した。トンボ目幼虫とカメムシ目成虫の個体数は植被率が高いほど増加したが、水生昆虫類の種数は植被率が高いほど減少した。したがって、複数の分類群の生息環境を創出するためには、代掻きや草刈りにより植生を管理し、水深に勾配をつけることが重要である。本研究は、水田やピオトープ、池を含む複数の生息環境を創出または維持することで、放棄された棚田における水生昆虫類の多様性を向上させることができることを示唆する。

Introduction

Since the 1950s, notable farmland abandonment has occurred in many developed countries in Europe, North America, Oceania, and Asia, including Japan and South Korea (Li and Li 2017). The driving forces of farmland abandonment are confirmed to be multiple socioeconomic factors: (1) the emigration of rural populations and reductions in farmers due to urbanization and industrialization; (2) declining agricultural benefits; (3) new agricultural policies; (4) land system reforms; and (5) new agricultural technologies and agricultural commercialization (Li and Li 2017). This trend continues in developing countries undergoing rapid socioeconomic changes (Díaz et al. 2011). Farmland abandonment can cause food security problems and biodiversity loss; however, some researchers view it as an opportunity for habitat regeneration, such as native forests and the restoration of natural grasslands in Europe (Queiroz et al. 2014).

Approximately 35% of wetlands worldwide have disappeared since the 1970s because of direct effects, such as diversion to farmland, afforestation, and urban development, and indirect effects, such as changes in water flow due to dam construction (Johnston 1994; van Asselen et al. 2013; Ramsar Convention on Wetlands 2018). In Japan, 61.1% of the wetlands in the Meiji and Taisho eras (1868–1926) have disappeared (Geospatial Information Authority of Japan 2000). The loss of wetlands directly leads to a decrease in wetlands and seminatural grassland species (Halis 1997; Craft 2022). Wetland and seminatural grassland species are using paddy fields and surrounding water bodies as alternative habitats due to the decline of natural wetlands (Nahara 2013). The area of paddy fields in Japan is 23,520 km², which is larger than that of natural wetlands (820 km²) (Geospatial Information Authority of Japan 2000; MAFF 2022). Therefore, paddy fields are important habitats for many organisms (Nisikawa and Miyashita 2014). In fact, 6,305 species have been recorded in paddy fields, agricultural ditches, and irrigation ponds (Kiritani and Otsuka 2020).

In Japan, the area of abandoned paddy fields has been rapidly increasing, mainly owing to low agricultural benefits, rural depopulation and aging since the 1980s (Katayama et al. 2015; Mameno and Kubo 2022). This tendency is remarkable in hilly and mountainous areas, where the mechanization of rice farming is often difficult because of small field sizes and steep slopes, and the risk of crop damage by

mammals is also high in these areas (Katayama et al. 2015). Hilly and mountainous areas cover approximately 70% of Japan's total land area, and rice terraces (*tanada* in Japanese) are the typical traditional paddy fields in these areas (Saito and Ichikawa 2014). Secondary succession in abandoned paddy fields makes recultivation difficult (Ohkuro et al. 2001) and causes biodiversity loss (Koshida and Katayama 2018). A meta-analysis of the effects of rice field abandonment on biodiversity in Japan revealed that species richness and abundance of organisms after abandonment decreased to 56–72%, and this reduced biodiversity was unlikely to recover, at least for plant species richness, even after 10–15 years (Koshida and Katayama 2018). According to Koshida and Katayama (2018), the negative effects of rice field abandonment on biodiversity are greater in complex landscapes (i.e., forested valleys (*yatsuda* in Japanese) and rice terraces) than in paddy fields situated in plains or lowlands.

Another problem is that the abandoned paddy field serves as a habitat for mammals damaging to crop such as wild boar (*Sus scrofa* Linnaeus, 1758) and sika deer (*Cervus nippon* Temminck, 1838) and promotes their invasion into surrounding farmlands (Honda 2007; Okumura et al. 2009). Indeed, the distribution area of these mammals expanded from 1978 to 2018, approximately 1.9 times for wild boar and 2.7 times for sika deer (Ministry of the Environment of Japan 2021). In addition, the risk of landslides and floods increases when paddy field soil dries out due to abandonment, especially in rice terraces (Ota et al. 1996; Nanbu et al. 2013). Thus, an increase in rice field abandonment is a crucial land use problem in Japan.

Under these domestic trends, fallow field biotopes (hereafter, biotopes) are attracting attention as a method to prevent an increase in abandoned paddy fields and to conserve biodiversity (Katayama et al. 2020). Biotopes are abandoned or fallow fields maintained by human disturbances, such as flooding and mowing (Nisikawa 2014). Indeed, a meta-analysis showed that flooded fallow fields have higher species and abundances of plants, insects (i.e., Lepidoptera, terrestrial Coleoptera, Lampyridae, Odonata, and Orthoptera), and birds than conventional paddy fields (Koshida and Katayama 2018). A systematic review reported that the conservation effectiveness of biotopes has been fully established for plants, invertebrates, amphibians, and birds (Katayama et al. 2020). Biotopes play a role in biodiversity conservation and environmental education in elementary schools in some areas of Japan, where nature observation classes

are conducted (Tabiraki 2017). However, the knowledge of effective management methods for maintaining the diversity of each taxonomic group is limited (Koshida and Katayama 2018; Katayama et al. 2020).

It is important to select appropriate indicators of biodiversity when determining effective management strategies for maintaining biodiversity in biotopes (Caro 2010). Aquatic insects (Odonata, Hemiptera, and Coleoptera) are one of the surrogate groups for biodiversity in newly created wetlands (Briers and Biggs 2003; Bilton et al. 2006; Sánchez-Fernández et al. 2006; Skern et al. 2010) because of following reasons (Fairchild et al. 2000; Lancaster and Downes 2013; Ohba 2019): (1) the dominant taxa in wetlands; (2) differentiation of microhabitat preference and diets (carnivorous, detritus, herbivorous, and omnivorous) for each species; (3) early colonizer in newly created wetlands; and (4) containing flagship and umbrella species such as the giant water bug, *Kirkaldyia deyrolli* (Vuillefroy, 1864). When creating biotopes, an increasing number of mosquitoes become disease vectors (O'Geen et al. 2010). These aquatic insects are important predators of mosquitoes (Shaalan and Canyon 2009), and the abundance of mosquito larvae in biotopes is lower than in paddy fields because of the high diversity of predatory aquatic insects (Ohba et al. 2013). Thus, aquatic insects are important for biodiversity monitoring and mosquito control in biotopes.

In contrast, aquatic insect diversity in Japanese paddy environments is rapidly declining because of multiple factors (Nishihara et al. 2006; Nishihara 2016; Watanabe and Ohba 2022): increased abandonment of paddy fields, farmland consolidation, use of pesticides and herbicides, abandonment and improvement of irrigation ponds, predation, resource competition, and habitat modification by invasive exotic animals. Indeed, 19% (18 of 97 species) in Odonata, 24% (17 of 72 species) in aquatic Hemiptera (Nepomorpha and Gerromorpha), and 40% (59 of 147 species) in aquatic Coleoptera (Elmidae, Dryopidae, Dytiscoidea, Hydrophilidae, Hydraenidae, Haliplidae, and Gyrinidae) that inhabits paddy environments are listed on the Red List of Japan (Kiritani and Otsuka 2020; Ministry of the Environment of Japan 2020). Therefore, their conservation is urgently required. Some studies have shown that biotopes function as habitats for aquatic insects and that their diversity declines 2–4 years after creation (Tanaka et al. 2013; Nakajima and Miyawaki 2021; Tawa and Sagawa 2022). However, there has been no quantitative study on whether biotopes cast a similar aquatic insect community colonized in the surrounding paddy fields and irrigation ponds, with a statistical comparison of community composition. This knowledge is necessary for the future management of abandoned paddy fields to determine whether those fields should be maintained as paddy fields as much as possible or whether biotopes would suffice for conserving aquatic insects.

We conducted field experiments on abandoned rice terraces in western Hyogo Prefecture, central Japan, to account for knowledge gaps in the management practices of abandoned paddy fields. Nine abandoned paddy fields were plowed and flooded and divided into three types: paddy fields, biotopes, and mixed fields (70% of the total area was managed as paddy field and 30% of that was biotope). We also surveyed surrounding irrigation ponds. We examined how the species richness, abundance, and community composition of aquatic insects differed among habitat types to assess the function of each habitat type as a habitat for aquatic insect communities.

Materials and Methods

Study Site

The study site was located on rice terraces in western Hyogo Prefecture, central Japan (Table 1; Fig. 1; Fig. S1, approximately 100 × 120 m), and nine paddy fields were abandoned and dried from 2019 to 2020 because of the absence of farmers. Before abandonment, aquatic insect diversity was high, whereas herbicides (granules of pyraclo-nil, pyriminobac methyl, and fenquinotrione, Kumiai Chemical Industry Co., Ltd., Tokyo), pesticides (granules of oxazosulfonyl and dichlobentiazox, Kumiai Chemical Industry Co., Ltd., Tokyo and granules of etofenprox and pyroquilon, Mitsui Chemicals Crop & Life Solutions, Inc., Tokyo), and a fungicide (fenitrothion emulsion, Kumiai Chemical Industry Co., Ltd., Tokyo) were used for rice cultivation. Ecological studies on water bugs have been conducted at the study site (Ohba et al. 2008, 2019; Ohba and Goodwyn 2010). We plowed and flooded these fields using a cultivator from mid-May 2023 and managed them as three field types: paddy fields (paddies 1–5, $n = 5$), biotopes (biotopes 1–3, $n = 3$), and mixed fields (mixed fields, $n = 1$) to recover the study site and consider the management practices of abandoned paddy fields. The water was first pulled from an irrigation pond (pond 1) to paddy 1 and then runoff from other fields from top to bottom through underground drainage. All fields had a ditch (32–54 cm wide) to warm the water drawn from the irrigation pond or upper field and prevent the rice plant, *Oryza sativa* (Poaceae), from blast disease. We flooded all the fields from May to August 2023 and drained them for harvesting in September by opening the lid of the pipe stuck in the ditch. After drainage, the water remained in the ditch until October 2023. Rice plants were cultivated in paddy fields from May to August 2023 and harvested in September 2023. For weed control in paddy fields, we utilized herbicides once just after planting but did not use any pesticides or fungicides. We did

Table 1 Description of the study site

Site	Field type	Surface area (m ²)			Water depth (cm; mean \pm SD)		Water temperature (°C)	DO (mg/L)	pH	Turbidity (NTU)	Vegetation Cover (%)
		Field	Ditch	Total	Field/Pond	Ditch/Max					
Paddy 1	Paddy field	240.4	13.5	253.9	3.8 \pm 2.7	15.0 \pm 10.2	31.1	9.35	8.56	10.7	18.8
Paddy 2	Paddy field	474.9	21.1	496.0	4.1 \pm 2.4	16.0 \pm 10.7	33.6	10.17	8.77	9.8	16.3
Paddy 3	Paddy field	234.8	10.7	245.5	5.8 \pm 3.4	13.6 \pm 8.5	34.5	9.17	8.39	9.2	2.6
Paddy 4	Paddy field	160.0	10.9	170.9	2.2 \pm 2.5	9.3 \pm 3.9	36.5	9.41	8.18	11.2	3.2
Paddy 5	Paddy field	210.2	6.1	216.3	6.0 \pm 1.8	9.9 \pm 7.7	35.3	9.38	8.43	11.2	2.9
Biotope 1	Biotope	175.7	11.0	186.7	5.9 \pm 1.2	18.0 \pm 11.1	32.9	8.42	7.32	29.0	38.8
Biotope 2	Biotope	207.4	14.3	221.7	5.8 \pm 1.8	18.7 \pm 7.2	34.1	11.60	9.98	5.3	26.1
Biotope 3	Biotope	185.4	9.8	195.1	3.6 \pm 2.0	4.4 \pm 3.3	34.9	7.93	8.17	33.8	35.9
Mixed field	Mixed field	288.6	23.5	312.1	7.5 \pm 2.1	25.5 \pm 18.3	32.7	8.98	7.62	31.4	11.2
Pond 1	Pond	-	-	223.7	29.0 \pm 3.7	54.7	26.0	7.06	7.46	1.9	0
Pond 2	Pond	-	-	46.8	15.5 \pm 4.8	25.4	25.9	5.38	7.05	7.9	73.1
Pond 3	Pond	-	-	109.3	28.9 \pm 6.6	50.3	25.1	5.27	6.69	8.5	29.7
Pond 4	Pond	-	-	45.1	35.7 \pm 7.7	128.5	21.5	0.57	6.76	9.8	90.9

The water parameters and vegetation cover were measured in June 2023

In the column 'Water depth,' 'Field/Pond' indicates measurements in the field of three field types (paddy fields, biotopes, and a mixed field) or shore of ponds, and 'Ditch/Max' indicates measurements in the ditch of the three field types or the center of the ponds. The water parameters were measured using a turbidity meter (TB-31, TOA-DKK Corp., Tokyo, Japan) and a pH/DO meter (LAQUA D-210PD, HORIBA, Ltd., Kyoto, Japan)

not cultivate rice plants or use herbicide in the biotopes, allowing weeds, mainly composed of rock bulrush, *Scheuchzeria palustris* (L.) L., marsh dewflower, *Murdannia keisak* (Hassk.) Hand.-Mazz., and the pickerel weed *Monochoria vaginalis* (Burm.f.) C.Presl ex Kunth, to flourish (Table S1). We managed 70% of the total area in the mixed field was similar to that of the paddy fields, and did not cultivate other areas because of the difficulty in using agricultural machines due to deep mud. Four irrigation ponds (ponds 1–4) were flooded throughout the year, and their water levels were stable during the study period. Floating and emergent plants were observed in ponds 2–4, but not in pond 1 (Table S1). The study site had a beautiful rice terrace landscape enjoyed by residents and tourists before abandonment. Therefore, we mowed plants onto the levees surrounding the fields in each survey to preserve the landscape (Fig. S2a). Ditches in all fields were dredged with mud in November 2022 to secure water for the study sites (Fig. S2b). No predatory fish or invasive exotic animals were observed at any of the study sites. The average (min–max) temperatures was 23.0 [18.6–28.8] °C, and average (min–max) of monthly total precipitation was 141.2 [61.5–226.0] mm during the study period (May to October 2023) in the study site (Japan Meteorological Agency 2024).

Aquatic insect species, particularly *K. deyrolli* are commonly collected for use as pets and for specimen collection in Japan, and collection pressure from traders and

enthusiasm is a contributing factor to the local population decrease (Nishihara 2016). *Kirkaldyia deyrolli* is designated as a specified class II nationally rare species of wild fauna and flora by the Act on Conservation of Endangered Species of Wild Fauna and Flora, which banned the capture or other actions regarding selling or distributing living individuals (Ministry of the Environment of Japan 2023). Therefore, we decided not to show the exact locations of the study sites to ensure the protection of these species.

Sampling of Aquatic Insect Communities

Aquatic insects (Odonata, Hemiptera, and Coleoptera) were sampled once a month from May to October 2023. Aquatic insects were collected by scraping the bottom of the water body with a D-framed net (30 cm wide, 1 mm mesh) 1 m from the water edge at ten randomly selected points in the ditch and five points in the paddy fields, biotopes, and a mixed field. Sampling was conducted in the ditch from May to October and in the field from May to August. However, we could not sweep five points in the field of paddy 4 in August and the ditch of paddy 5 from September to October because of the lack of water. The ponds had a water depth gradient and the sampling method was changed to capture aquatic insects in deeper water comprehensively. We scraped the bottom of the water body in the ponds with a D-frame net 1 m from the center of the pond to the shore at ten randomly selected

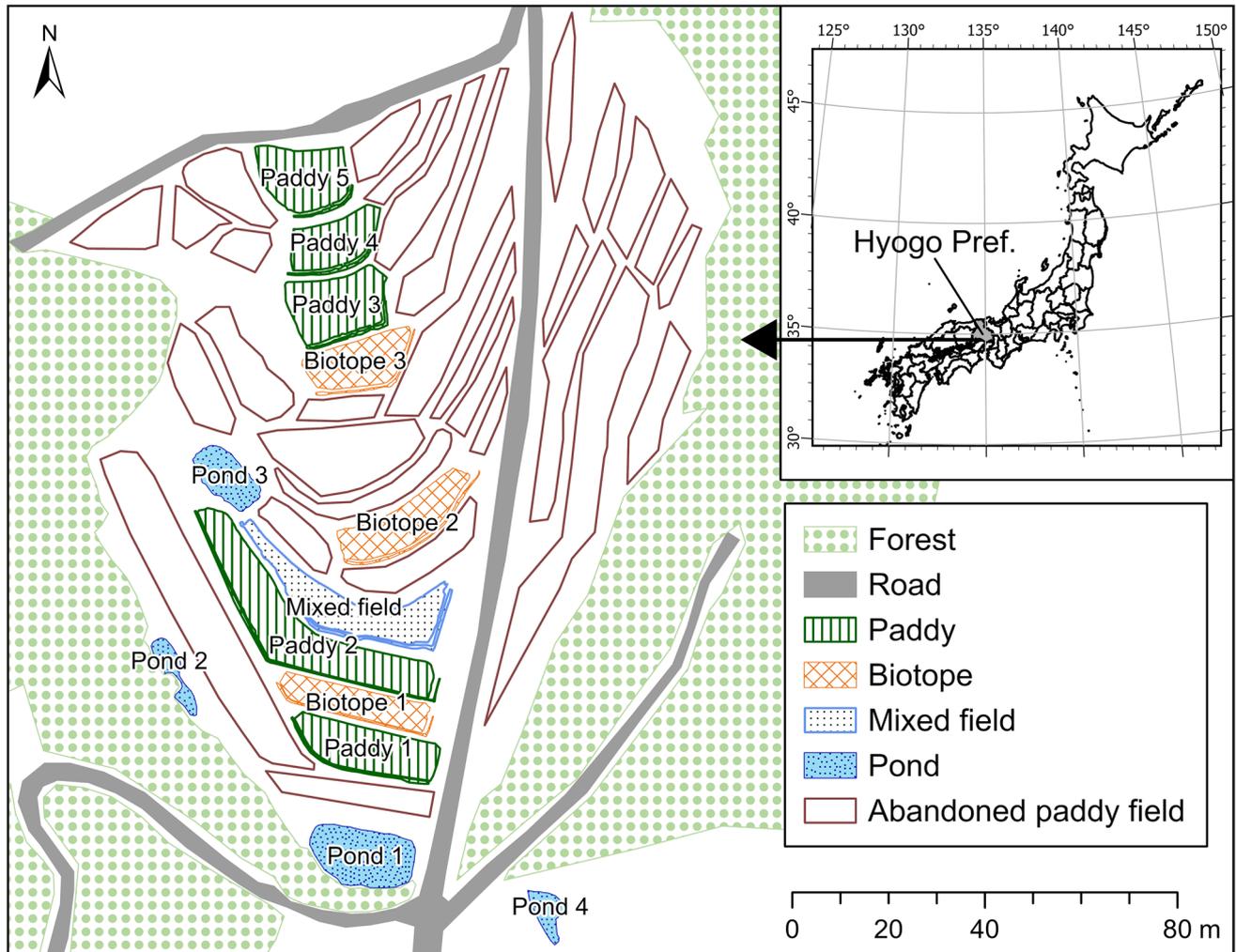


Fig. 1 The location of the study site in western Hyogo Prefecture, central Japan

points. We recorded the abundance of each species and their life stage (adult or larva/nymph) by sweeping, after which the individuals were released at the collection site. To avoid double counting, the distance between sampling points was at least 1.5 m. We recorded the abundance of several unidentified species of the same genus (i.e., *Lestes* spp., *Paracercion* spp., *Ischnura* spp., *Trigomphus* spp., *Sympetrum* spp., *Appasus* spp., *Microvelia* spp., *Sigara* spp., and *Parapleia* spp.) as one species, as small individuals, females, and larvae/nymphs could not be distinguished because of the lack of identification keys. Aquatic insects that could not be identified in the field were preserved in 70% ethanol and brought to the laboratory for identification using identification keys (Kawai and Tanida 2018; Nakajima et al. 2020; Umeda 2023).

Environmental Factors

We measured the water depth at 30 cm from the water edge at four randomly selected points in the ditch and field at each site in the paddy fields, biotopes, and mixed fields, using a folding ruler (5–folding 1 m, Shinwa Rules, Niigata) from May to October, except for June. Similarly, we measured the water depth at 30 cm from the water edge at four randomly selected points and at the center of the ponds once in April 2023 because the water level was stable during the study period.

Flying aquatic insects locate water bodies using reflected polarized light (Schwind 1995); therefore, we hypothesized that a large surface area promotes and high vegetation cover would hinder the colonization of aquatic insects. Vegetation cover refers to the percentage of the area covered by floating and emergent plants on the water

surface. We captured aerial images using an unmanned aerial vehicle (DJI mini2, DJI, Shenzhen) in June 2023, during the breeding season of almost all aquatic insects, to measure the surface area (m²) and vegetation cover of each site (Saijo 2001). The aerial images were orthorectified, and the surface areas of the water bodies and vegetation cover were measured using ArcGIS Pro (ver. 3.1.0, ESRI, USA) and ImageJ software (Abràmoff et al. 2004), respectively. The surface area was pooled for the field and ditch in the paddy fields, biotopes, and mixed fields, and the vegetation cover was only measured in the field because the ditch was shaded by terrestrial plants.

Statistical Analysis

We used the statistical software R version 4.1.0 for all analyses (R Core Team 2023). We performed non-metric multidimensional scaling (NMDS) based on the matrix of total abundance of each species throughout the study period to compare aquatic insect communities among the paddy fields, biotopes, and mixed fields. We used the metaMDS function in the ‘vegan’ package (Oksanen et al. 2020). The analysis was performed using the Morisita–Horn index, which effectively controls for differences in sample size (Doi and Murakami 2011). We assessed whether the stress value of the biplot was < 0.2 to evaluate the goodness-of-fit of the NMDS (Kruskal 1964). We performed a permutation analysis of variance (PERMANOVA) with the Morisita–Horn index (10,000 permutations) using the matrix of total abundance of each species throughout the study period at 12 sites, except for the mixed field, to determine the differences in the composition of aquatic insect communities among paddy fields, biotopes, and ponds. We used the adonis2 function in the ‘vegan’ package (Oksanen et al. 2020). In this model, we incorporated habitat type (paddy field, biotope, or pond), surface area, average water depth of the ditch/pond, and vegetation cover as fixed effects. We performed the IndVal analysis (1,000 randomizations) using the indval function in the ‘labdsv’ package (Roberts 2023) to identify the dominant species within each habitat type. This analysis estimated indicator values based on the relative abundance and frequency of occurrence of each species in each habitat type.

We used a generalized linear model (GLM) to compare the total abundance and species richness of aquatic insects throughout the study period among habitat types (Ripley et al. 2024). We used a negative binomial distribution using the glm.nb function in the ‘MASS’ package and a Poisson distribution using the glm package for the total abundance and the species richness, respectively. Habitat type, surface area, average water depth of the ditch/pond, and vegetation cover were incorporated as explanatory variables. For the NMDS, PERMANOVA, and GLMs, the abundances were pooled for life stages (adult and larva/nymph) and sampling site (ditch

and field in paddy fields, biotopes, and a mixed field). We also created ten GLMs for the total abundance with a negative binomial and species richness with a Poisson distribution of each order and life stage as response variables and habitat type, surface area, average water depth of the ditch/pond, and vegetation cover were incorporated as explanatory variables.

The log-transformed sweeping effort (i.e., the number of times sweeping was undertaken) was incorporated as an offset to account for the differences in sampling efforts in the GLMs. We created models for all possible combinations of explanatory variables and calculated the Akaike information criterion (AIC) value for each model. The model with the lowest AIC value was selected as the best. We calculated the 95% confidence intervals (CI) for estimated coefficients of the best model by using the model parameters function in the ‘parameters’ package (Lüdecke et al. 2023a). Prior to the GLMs, the explanatory variables in full models were tested for multicollinearity by calculating the variance inflation factor (VIF, Dormann et al. (2013)) using the check_collinearity function in the ‘performance’ package (Lüdecke et al. 2023b), and we confirmed that the VIF was less than 5 (Table S2). Interactions between the explanatory variables were not incorporated into the aforementioned models because the sample size was small (n = 12) or multicollinearity was detected when interaction terms were incorporated as explanatory variables (VIF > 5). In addition, we performed a dispersion test by using the odTest function in the ‘pscl’ package (Jackman et al. 2023) and confirmed that over-dispersion did not occur in the best models with a negative binomial distribution.

Results

We recorded 58 species and 11,591 individuals of aquatic insects (Odonata: 22 species and 3854 individuals; Hemiptera: 20 species and 7169 individuals; Coleoptera: 16 species and 568 individuals) at the study sites (Table S3; Fig. S3a); a total of 45 species and 3225 individuals (Odonata: 19 species and 1432 individuals, Hemiptera: 14 species and 1604 individuals, Coleoptera: 12 species and 189 individuals) in paddy fields; 43 species and 1986 individuals (Odonata: 18 species and 574 individuals, Hemiptera: 13 species and 1229 individuals, Coleoptera: 12 species and 183 individuals) in the biotopes; 38 species and 1500 individuals (Odonata: 15 species and 322 individuals, Hemiptera: 13 species and 1125 individuals, Coleoptera: 10 species and 53 individuals) in a mixed field; and 52 species and 4880 individuals (Odonata: 20 species and 1526 individuals, Hemiptera: 20 species and 3211 individuals, Coleoptera: 12 species and 143 individuals) in ponds (Table S3; Fig. S3b–e).

A total of 34 species were observed in all habitat types, but one species in a mixed field, two species in both paddy fields and biotopes, and nine species in ponds were found

only in one habitat type (Table S3; Fig. S4). In total, 10 species are included in the Red List of Japan (Table S3).

Factors Influencing the Community Composition of Aquatic Insects

Community composition of aquatic insects was significantly affected by habitat type and vegetation cover (Table 2; Fig. 2). In contrast, surface area and water depth did not significantly affect community composition. Three indicator species were identified in the paddy fields: the water scorpion *Laccotrephes japonensis* Scott, 1874, diving beetle *Hydaticus grammicus* (Germar, 1827), and white-tailed skimmer *Orthetrum albistylum* (Selys, 1848) (Table 3). The only indicator species of the biotopes was the water-scavenger beetle *Enochrus simulans* (Sharp, 1873). In the ponds, three Odonata species (*Paracercion* spp., *Lestes* spp., and *Pseudothemis zonata* (Burmeister, 1839)), the water treader *Mesovelgia* sp., the backswimmer *Notonecta triguttata* Motschulsky, 1861, and the water strider *Gerris latiabdominis* Miyamoto, 1958 were detected as indicator species.

Factors Influencing the Abundance and Species Richness of Aquatic Insects

For the total abundance of aquatic insects, the best model included habitat type, surface area, water depth, and vegetation cover as explanatory variables. The total abundance of aquatic insects was higher in ponds than paddy fields and biotopes (Table S4a; Fig. 3a), increased with surface area (Table S4a; Fig. 3b) but decreased with water depth (Table S4a, Fig. 3c). In contrast, the best model of total species richness had habitat type and vegetation cover as explanatory variables. The species richness of aquatic insects was higher in ponds than paddy fields (Table S4b; Fig. 3d) and decreased with increasing vegetation cover (Table S4b ; Fig. 3e). The 95% CI of estimated coefficient on vegetation cover included zero in abundance (Table S4a).

The abundance of Odonata nymphs was higher in paddy fields than in biotopes and ponds and increased with water depth and vegetation cover (Table 4). The species richness of Odonata nymphs and Hemiptera adults increased with water depth but decreased with vegetation cover (only for Hemiptera adults). The 95% CI of estimated coefficient on habitat type included zero in the species richness of Hemiptera nymphs. The abundance of Hemiptera nymphs and adults and the abundance and species richness of Coleoptera larvae were higher in biotopes and ponds than in paddy fields and increased with surface area and decreased with water depth (except for Hemiptera adults) and vegetation cover (except for Hemiptera adults and Coleoptera larvae). The abundance and species richness of Coleoptera adults were higher in the biotopes and ponds (only in abundance) than in the paddy fields.

Table 2 Effects of the habitat type and structures on aquatic insect communities using permutational multivariate analysis of variance (PERMANOVA) with Morisita–Horn index

	Df	Sum of sqs	R ²	pseudo-F	p-value
Habitat type	2	1.09	0.64	12.69	< 0.01
Surface area	1	0.04	0.02	0.92	0.45
Water depth	1	0.14	0.08	3.21	0.07
Vegetation cover	1	0.19	0.11	4.31	0.03
Residuals	6	0.26	0.15		

Significant results are shown in bold ($p < 0.05$)

Discussion

We investigated the aquatic insect communities of paddy fields, biotopes, a mixed field, and irrigation ponds and examined the factors that influence the community composition, abundance, and species richness of aquatic insects. We found that the aquatic insect assemblages of biotopes differed from paddy fields and irrigation ponds and resembled that of a mixed field (Table 2; Fig. 2). Of the 58 species in the study site, one species in a mixed field, two species in both paddy fields and biotopes, and nine species in ponds were found only in that specific habitat type (Table S3; Fig. S4). These results indicated that the combination of different habitat types increases aquatic insect diversity in paddy environments, even at the investigated scale (~100 × 120 m). Nakajima and Miyawaki (2021) compared the species richness of aquatic Hemiptera and Coleoptera between biotopes and ponds and reported that nine species that preferred ponds with abundant aquatic plants were not found in biotopes, even nine years after their creation. Watanabe (2016) also confirmed that the community composition of aquatic Hemiptera and Coleoptera differed between paddy fields and adjacent agricultural ditches.

In general, three principal mechanisms enhance species richness in mosaic landscapes, such as paddy environments (Miyashita et al. 2014). First, the presence of different habitat types results in high beta diversity, which represents the turnover of species composition between different habitats or between habitat diversity because different habitats harbor different species assemblages in response to different environmental conditions (Miyashita et al. 2014). Indicator species analysis revealed the dominant species in each habitat type, and the results corresponded to the habitat preferences reported in previous studies. Three indicator species were identified in the paddy fields: the water scorpion, *L. japonensis*; the diving beetle, *H. grammicus*; and the white-tailed skimmer, *O. albistylum*. *L. japonensis* uses both paddy fields and ponds for reproduction and overwintering; however, the survival rate of nymphs is higher in paddy fields (Ohba and Goodwyn 2010).

Fig. 2 Non-metric multidimensional scaling (NMDS) analysis of aquatic insect community composition among paddy fields, biotopes, a mixed field, and ponds using the Morisita–Horn index. Orange, green, and blue ellipses indicate the standard deviation of points of paddy fields, biotopes, and ponds, respectively

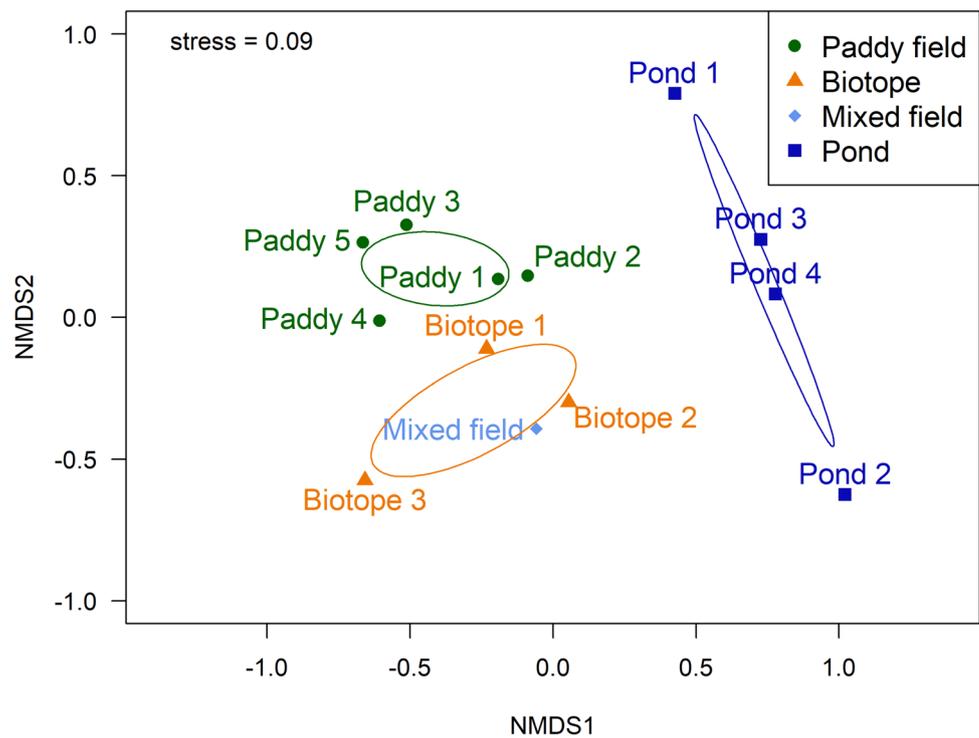


Table 3 Indicator species for each habitat type using indicator value analysis

Order	Family	Indicator species	Habitat type	Relfrq	Relabu	IndVal	p-value
Hemiptera	Nepidae	<i>Laccotrephes japonensis</i>	paddy	1.00	0.66	0.66	0.04
Coleoptera	Dytiscidae	<i>Hydaticus grammicus</i>	paddy	1.00	0.65	0.65	0.01
Odonata	Libellulidae	<i>Orthetrum albistylum</i>	paddy	1.00	0.61	0.61	<0.01
Coleoptera	Hydrophilidae	<i>Enochrus simulans</i>	biotope	1.00	0.83	0.83	0.02
Odonata	Coenagrionidae	<i>Paracercion</i> spp.	pond	1.00	0.97	0.97	<0.01
Odonata	Lestidae	<i>Lestes</i> spp.	pond	1.00	0.92	0.92	<0.01
Odonata	Libellulidae	<i>Pseudothemis zonata</i>	pond	1.00	0.75	0.75	0.03
Hemiptera	Mesoveliidae	<i>Mesovelia</i> sp.	pond	0.75	1.00	0.75	0.02
Hemiptera	Notonectidae	<i>Notonecta triguttata</i>	pond	1.00	0.68	0.68	<0.01
Hemiptera	Gerridae	<i>Gerris latiabdominis</i>	pond	1.00	0.58	0.58	0.01

'Relfrq' and 'Relabu' indicates the relative frequency and abundance of indicator species in each dominant habitat type

Previous studies have also reported that *H. grammicus* and *O. albistylum* mainly inhabit paddy fields (Uéda 1998a; Nakajima et al. 2020). Tawa and Sagawa (2022) showed that the abundance of *O. albistylum* nymphs is higher in paddy fields than in biotopes and agricultural ditches. The only indicator species of biotopes was the water scavenger beetle, *E. simulans*, which prefers shallow and highly vegetated wetlands (Nakajima et al. 2020), and this environmental condition was confirmed in the biotopes (Table 1). Three Odonata species (*Paracercion* spp., *Lestes* spp., and *P. zonata*), the water treader *Mesovelia* sp., the backswimmer *N. triguttata*, and the water strider *G. latiabdominis* were detected as indicator species in ponds, which are related to

water depth and floating and emergent plants. Two damselfly species (*Paracercion* spp. and *Lestes* spp.) oviposit on the stems of floating and emergent plants in ponds, and *P. zonata* prefers ponds to paddy fields (Uéda 1998b; Kadoya et al. 2004; Umeda 2023). The water treader inhabits ponds flourishing with floating plants, such as *Trapa japonica* Flerow, 1925 (Nakajima et al. 2020), and *N. triguttata* prefers ponds with deep-water depths (Saijo 2001; Tawa and Sagawa 2022). In contrast, *G. latiabdominis* prefers shallow and open wetlands such as paddy fields (Nakajima et al. 2020). Therefore, other factors might affect its abundance, such as the abundance of prey and predators (Spence and Andersen 1994).

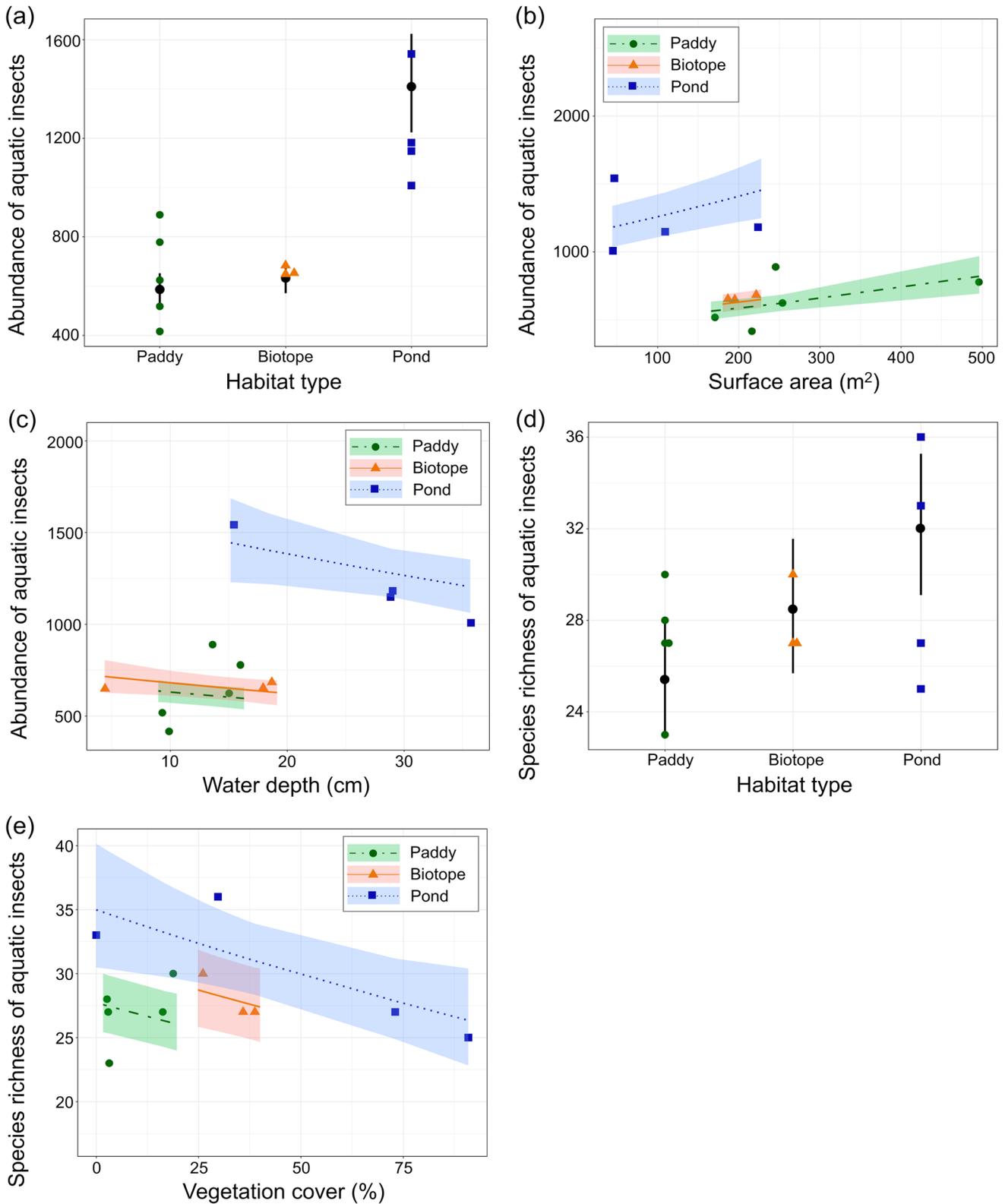


Fig. 3 Predicted regression of (a)–(c) abundance and (d, e) species richness in the best models with generalized linear models. Black bars (a, d) and filled areas (b, c, e) indicate the 95% confidence intervals of the estimates

Table 4 Estimated coefficients [lower CI to upper CI] of the best model with generalized linear models for abundance and species richness of aquatic insects in each life stage

Order	Life stage	Response variable	Explanatory variable				
			Habitat type (biotope)	Habitat type (pond)	Surface area	Water depth	Vegetation cover
Odonata	Nymph	Abundance	-0.66 [-0.83 to -0.49]	-0.39 [-0.66 to -0.12]	-0.0006 [-0.0014 to 0.0001]	0.02 [0.01 to 0.03]	0.63 [0.33 to 0.93]
		Species richness				0.013 [0.003 to 0.022]	
Hemiptera	Nymph	Abundance	0.46 [0.21 to 0.71]	1.42 [1.02 to 1.82]	0.0014 [0.0002 to 0.0026]	-0.03 [-0.05 to -0.02]	-0.52 [-0.97 to -0.08]
		Species richness	-0.18 [-0.43 to 0.05]	0.08 [-0.12 to 0.29]			
	Adult	Abundance	0.31 [0.12 to 0.50]	1.57 [1.27 to 1.87]	0.002 [0.001 to 0.003]	-0.012 [-0.024 to 0.00005]	0.48 [0.14 to 0.82]
Coleoptera	Larva	Species richness				0.02 [0.01 to 0.03]	-0.59 [-0.96 to -0.22]
		Abundance	1.21 [0.84 to 1.58]	1.69 [1.10 to 2.29]	0.004 [0.003 to 0.006]	-0.03 [-0.06 to -0.01]	
		Species richness	0.50 [0.10 to 0.91]	1.08 [0.41 to 1.75]	0.003 [0.001 to 0.005]	-0.04 [-0.07 to -0.02]	
	Adult	Abundance	0.92 [0.56 to 1.28]	0.77 [0.33 to 1.21]	0.005 [0.003 to 0.006]		
		Species richness	0.34 [0.07 to 0.62]	0.20 [-0.14 to 0.54]	0.001 [-0.0002 to 0.002]		

Significant results are shown in bold (95% CI does not include zero)
 The estimates of habitat type (paddy, biotope, or pond) are based on the category of “paddy”

The second mechanism that enhances species diversity in paddy environments is periodic disturbances by human activities (e.g., mowing of grasses on levees, plowing before rice plantations, dredging mud in ditches, and drying ponds), which prevent secondary succession in wetlands, allowing multiple species to coexist under non-equilibrium ecological conditions (Miyashita et al. 2014). At the study site, we plowed and utilized herbicides in paddy fields for weed control but not in biotopes and ponds. This caused a difference in vegetation cover during the breeding season of aquatic insects (Table 1), influencing the community composition of aquatic insects (Table 2). This is in line with previous studies that showed vegetation structure affects aquatic insect assemblages, for example, aquatic Coleoptera in flood plains (Turić et al. 2021), aquatic insects in irrigational ponds (Nakanishi et al. 2014), and Odonata in constructed agricultural wetlands (Huikkonen et al. 2020). The importance of human disturbances in biotopes for maintaining aquatic insect diversity has been previously pointed out. The species richness of aquatic insects in biotopes declined 2–4 years after creation because of mud accumulation, declining species richness of aquatic plants, and the invasion of predatory exotic animals (Tanaka et al. 2013; Nakajima and Miyawaki 2021). To counterbalance the decline in aquatic insect diversity over time, Suzuki et al. (2018) showed that drying in winter enhanced the taxa richness and abundance of macroinvertebrates, especially pioneer species, and altered their assemblages in biotopes. Tanaka et al. (2013) dredged mud from the bottom of a biotope during winter, which resulted in an increase in the richness of aquatic insect species. Therefore, agricultural management would contribute to maintaining aquatic insect diversity, such as plowing in the field and dredging mud in ditches.

Third, many aquatic insect species require multiple habitats to complete their life cycles (Uéda 1998a, b; Saijo 2001, 2002). The divergence in habitat use is caused by environmental factors in paddy environments (Uéda 1998a, b; Saijo 2001, 2002). We found that the effects of environmental factors differed according to order and life stage (Table 4). The abundance of aquatic insects, especially Hemiptera, was higher in ponds than in paddy fields and biotopes (Table 4; Fig. 3a), mainly because of the high abundance of the pygmy backswimmer *Paraplea* spp., the backswimmer *Anisops ogasawarenis* Matsumura, 1915, and the water crickets *Microvelia* spp. (Fig. S3e). Hemipteran nymphs and Coleoptera larvae were more abundant in the biotopes and ponds than in the paddy fields, and the species richness of Coleoptera larvae was higher in the biotopes and ponds than in the paddy fields (Table 4; Table S3). In contrast to our results, Tawa and Sagawa (2022) reported that aquatic Coleoptera collected from biotopes were mostly adults and that their larvae were observed in paddy fields and agricultural ditches. This different response of Coleoptera larvae

would be influenced by the flooding period of biotopes; the present study: May to August in the field and May to October in the ditch, Tawa and Sagawa (2022): all year around in the field. Brock et al. (2003) showed that drying events are crucial cues for zooplankton to hatch eggs from wetlands. Therefore, prey animals such as zooplankton could be more abundant in our designed temporary biotopes than in the permanent biotopes, resulting in an increase in the abundance and/or species richness of predatory Hemiptera nymphs and Coleoptera larvae (Pintar and Resetarits 2017). Saijo (2001) also confirmed that more species of aquatic Hemiptera and Coleoptera reproduce in paddy fields than in irrigation ponds and discussed one of the reasons for this as the lack of prey animals in irrigation ponds. The relationship between the duration of flooding and the abundance of prey animals and predatory aquatic insects must be clarified through field experiments to support our hypothesis.

In contrast, the abundance of Odonata nymphs was higher in paddy fields than in biotopes and ponds (Table 4), mainly due to *O. albistylum*, *Sympetrum* spp. and *Pseudocoptera annulata* (Selys, 1863) (Fig. S3b). One possible reason for this is that the abundance of Odonata nymphs in biotopes and ponds decreases with the abundance of their predators, such as aquatic Coleoptera and Hemiptera (Corbert 2004). It is necessary to describe the predator-prey relationships of aquatic insects in paddy environments using a combination of laboratory prey-choice experiments for a detailed analysis (Klecka and Boukal 2012) and stable isotope analysis (Ohba et al. 2019). On the other hand, the paddy fields surveyed in this study were different from conventional paddy fields; the former was applied with only herbicide application at once, while the latter is usually applied with multiple treatments of herbicides, insecticides and fungicides. In Japan, Odonata species, especially *Sympetrum* spp. decline their populations due to pesticide applications in conventional paddy fields (Nakanishi 2018; Nakanishi et al. 2019). Therefore, the habitat value of conventional paddy fields may be lower than that of the surveyed paddy fields.

The abundance of aquatic insects, especially Hemiptera and Coleoptera, increased with increasing surface area (Table 4; Fig. 3b). Our results are consistent with those of previous studies that reported a significant relationship between surface area and aquatic insect diversity, for example, the abundance of macroinvertebrates in garden ponds (Hill et al. 2023) and assemblages of aquatic Hemiptera and Coleoptera in artificial ponds (Apinda Legnoux et al. 2014).

The total abundance of the aquatic insects decreased with increasing water depth (Table S4a; Fig. 3c). In general, shallow wetlands tend to be warmer, leading to an increase in the biomass of algae, water plants, phytoplankton, zooplankton, and other invertebrates that are food resources for aquatic insects (Williams 2006). Therefore, the abundance of aquatic insects may increase in shallower waters because of

increased food resources. We found that the total abundance and species richness of aquatic insects were higher in ponds with deep water than paddy fields and/or biotopes (Table S4; Fig. 3a, d). Within ponds, the abundance of aquatic insects decreased with increasing water depth (Table S4a; Fig. 3c). These results indicate that the interaction between habitat type and water depth might affect the total abundance of aquatic insects, whereas we could not include the interaction term as an explanatory variable in the GLM due to small sample size ($n = 12$). In contrast, the total abundance and species richness of Odonata nymph increased with increasing water depth (Table 4). Deeper water depths may facilitate the coexistence of multiple species due to vertical niche partitioning, as observed in diving beetles (Pitcher and Yee 2014). Tawa and Sagawa (2022) investigated the aquatic insect community in a biotope with shallow water (mean = 10 cm) and partially deep water (max. = 80 cm) and confirmed that the abundance of some species was higher in deep water, including the odonatan nymph, *Epophthalmia elegans* (Brauer, 1865), the water stick insect, *Ranatra chinensis* Mayr, 1865; and the diving beetle, *Eretes griseus* (Fabricius, 1781). Thus, the creation of a water depth gradient, such as in deep zones (Tawa and Sagawa 2022) and ditches (Watanabe 2016), could contribute to enhancing aquatic insect diversity in biotopes.

The abundance of Odonata nymphs and Hemiptera adults increased with increasing vegetation cover (Table 4). This trend is consistent with previous studies on Odonata nymphs (Remsburg and Turner 2009; Huikkonen et al. 2020; Chen et al. 2020; Kolar et al. 2021) and aquatic Hemiptera (Karaouzas and Gritzalis 2006). The floating and emergent plants can serve as perching sites, hiding places from predators, foraging ground, and oviposition sites for adults of Odonata (Corbert 2004; Grof-Tisza et al. 2017) and Hemiptera (Nakajima et al. 2020). However, the abundance of Hemiptera nymphs and the species richness of aquatic insects, especially Hemiptera adults decreased with vegetation cover (Tables 4, S4; Fig. 3e). High vegetation cover may decrease the abundance of Hemiptera nymphs by increasing the abundance of their predators, the Odonata nymphs (Ohba 2007; Klecka 2014). In addition, high vegetation cover may decrease the predation efficiency of carnivorous Hemiptera species and lead to a decrease in species richness. A negative association with vegetation cover and a positive association with surface area were interpreted as possibly supporting the notion that open and large wetlands were more visible from the air than small and vegetated wetlands. In support of this interpretation, Wahl et al. (2021) reported that covering the water surface with invasive floating ferns limited aerial colonization and decreased the abundance and species richness of aquatic insects. In addition, Briggs et al. (2019) confirmed that well-vegetated ponds could enhance the species richness of Odonata nymphs and Coleoptera, although this decreased in

ponds dominated by a single plant at high densities. Therefore, a mosaic of aquatic vegetation in different successional stages could enhance aquatic insect diversity in biotopes as reported in previous studies (Huikkonen et al. 2020; Kolar et al. 2021).

Surrounding landscapes, such as forests, also determine aquatic insect assemblages in paddy field ecosystems because forests serve as overwintering sites and source habitats for prey animals (Kadoya et al. 2008; Raebel et al. 2012; Watanabe et al. 2019). Indeed, the surrounding forest and wetland cover within 2–3 km increase the abundance and/or taxon richness of aquatic Hemiptera and Coleoptera in paddy fields (Watanabe et al. 2019). In contrast, the presence of a large forest area within 200 m of the edge of a paddy field reduced the abundance of *Sympetrum infuscatum* (Selys, 1883) adults prefer open habitats (Baba et al. 2019). However, the present study did not consider the effects of prey abundance on the community composition of carnivorous aquatic insects (see also Watanabe et al. 2019). In addition, the surveyed sites were spatially aggregated within a small area, spatial autocorrelation may play a role in determining species compositions and diversity metrics. A comprehensive study is required to examine the effects of landscape and local environmental factors on aquatic insect communities in large-scale landscapes and plan the appropriate spatial arrangement and management practices of biotopes to maintain meta-populations.

Conclusions

With the notable increase in rice field abandonment, biotopes are attracting attention as a method to prevent an increase in abandoned paddy fields and conserve biodiversity. Our study revealed that aquatic insect assemblages of biotopes differed between paddy fields and irrigation ponds and that biotopes functioned as breeding sites for various abundant aquatic insect species, especially Hemiptera and Coleoptera. We also confirmed that the effects of environmental factors on the abundance and species richness of aquatic insects differed according to their order and/or life stages. The abundance of aquatic insects increased with surface area. The abundance of Odonata nymphs increased with water depth, whereas that of Hemiptera nymphs and Coleoptera larvae decreased. The abundance of Odonata nymphs and Hemiptera adults increased with increasing vegetation cover, whereas the species richness of aquatic insects decreased. Thus, it is important to prevent high vegetation cover by plowing and create a water depth gradient for creating habitats for multiple taxa. In conclusion, we suggest that creating or maintaining mosaic habitats, including paddy fields, biotopes, and ponds could enhance aquatic insect diversity in abandoned rice terraces.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13157-024-01823-6>.

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Author Contribution Reiya Watanabe: Conceptualization, methodology, investigation, validation, data curation, formal analysis, visualization, writing - original draft. Sho Kubo, Taichi Fukuoka, Kazukiyo Kobayashi, and Shinji Takahashi: Investigation, writing - review & editing. Shin-ya Ohba: Conceptualization, investigation, validation, funding acquisition, writing - review & editing.

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Data Availability The datasets in the current study are available from the supporting information (ESM1).

Declarations

Animal Research The authors carried out the research in accordance with the guidelines for animal experimentation.

Utilization of Plants This study is not applicable.

Competing Interests All the authors declared that they have no conflict interest to disclose.

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