Ecological value of gravel pit ponds for floodplain wetland fish

Honoka Nakahashi[1,a,*], Taihei Yamada[1,2,*], Nobuo Ishiyama[3], Futoshi Nakamura[1]

[1]Graduate School of Agriculture, Hokkaido University, N9 W9, Sapporo, Hokkaido 060-8589, Japan

[2]Higashitaisetsu Museum, 48-2 Nukabira-Gensenkyo, Kamishihoro, Hokkaido 080-1403, Japan

[3]Forest Research Institute, Hokkaido Research Organization, Bibai, Hokkaido, 079-0198, Japan

[a]Present address: ZENKIGEN, Inc. The 6 floor, Otemachi building, 1-6-1, Otemachi, Chiyodaku, Tokyoto 100-0004, Japan

[*]**Honoka Nakahashi and Taihei Yamada should be considered joint first authors**

Corresponding author: Taihei Yamada; E-mail, thymd8@gmail.com; TEL, +818039994855, Graduate School of Agriculture, Hokkaido University, N9W9, Sapporo, Hokkaido 060-8589, Japan

Keywords: artificial ecosystem, biodiversity, habitat loss, habitat restoration, threatened species

ABSTRACT

1. Floodplain wetlands support high biodiversity, but they have been degraded and geographically fragmented due to human activities. Some types of human-created waterbodies have received growing attention as alternative habitats for conserving wetland biodiversity. Gravel pit ponds (GPPs) are human-created wetlands formed when a gravel pit is excavated at or below the water table and filled with groundwater. Differences in community structure among GPPs and floodplain wetlands with respect to habitat characteristics are scarcely known, resulting in insufficient evaluations of the ecological value of GPPs for floodplain wetland species. In this study, we evaluated the ecological value of GPPs for wetland fishes in floodplain landscapes.
2. We surveyed fish abundance, community composition and ten environmental factors in GPPs and two types of floodplain ponds (remnant ponds and river backwaters) to clarify the biotic and abiotic differences among the pond types.
3. Environmental factors were similar among the pond types, with only water temperature and the distance from the main channel to the pond significantly lower in river backwaters. The richness and abundance of native fish species did not differ among the pond types, but species composition did. *Rhynchocypris percnura sachalinensis*, *Carassius* sp., and *Lethenteron* sp. N (one of the two cryptic species of *Lethenteron reissneri*) were selected as indicator species in GPPs, remnant ponds and river backwaters, respectively.
4. These results indicate that GPPs provide valuable habitats for wetland fishes in floodplain landscapes and support regional gamma diversity. Since many species inhabited the GPPs in this study, including red list species, appropriate management

of GPPs is important to conserve wetland fishes.

1. INTRODUCTION

Natural floodplain wetlands are among the most diverse and productive ecosystems on Earth (Keddy et al., 2009; Kingsford, 2000; Tockner & Stanford, 2002). However, loss and degradation of floodplain wetlands have occurred around the world because of human activities (Davidson, 2014; Hein et al., 2016; Kingsford, 2015; Reis et al., 2017; Tockner & Stanford, 2002), including river regulation, river channelization, and conversion to agricultural land (Fickas et al., 2016; Kingsford et al., 2016; Kuiper et al., 2014; Wilcock & Essery, 1991). The degradation of floodplains leads to a serious decline in the abundance of floodplain wetland species (Poff et al., 1997). Conservation of remnant natural or seminatural wetlands is one possible measure for the mitigation of biodiversity decline. However, this conventional measure cannot be applied to the areas wherein remnant natural and seminatural wetlands are seriously decreasing due to land use development; therefore, alternative habitats should be considered to develop conservation plans for wetland biodiversity.

The utilization of human-created wetlands is an alternative measure for the conservation of declining wetland biodiversity. Recent studies have shown that human-created wetlands (e.g., channelized watercourses, flood-control basins, and drainage pumping stations) function as habitats for wetland species (Chester & Robson, 2013; Ishiyama et al., 2022; Yamanaka et al., 2020). Conserving various wetlands, including human-created wetlands, may increase the gamma diversity of wetland species in the whole region because human-created waterbodies can support unique aquatic communities (Ishiyama et al., 2016; Yamanaka et al., 2020). These ecological advantages of human-created wetlands can contribute to wetland species conservation.

Gravel pit ponds (GPPs) are a type of human-created wetland where gravel pits are excavated at or below the water table, fill with groundwater and become artificial lakes (Mollema & Antonellini, 2016). Most GPPs are located in urban or agricultural settings (Mollema & Antonellini, 2016). Globally, the demand for sand and gravel is increasing, largely due to urban expansion, infrastructural improvements and the enhancement of coastal protection (Bendixen et al., 2019). Given the increased demand for geomaterials, the construction of GPPs may continuously increase in the future. Diverse organisms, such as fish, birds, plants, zooplankton, and macroinvertebrates, inhabit GPPs (including gravel pit lakes) (Emmrich et al., 2014; Santoul et al., 2009; Seelen et al., 2021; Søndergaard et al., 2018; Vucic et al., 2019; Zhao et al., 2016). Previous studies on human-altered floodplain landscapes have examined the difference in macrophyte community structures between GPPs and other pooled water bodies, including artificial canals and natural lakes. For example, Seelen et al. (2021) have suggested that GPPs have lower nutrient and chlorophyll-a concentrations, as well as unique macrophyte communities, compared with pooled water bodies. However, knowledge of the differences in community structure among GPPs and floodplain wetlands with respect to habitat characteristics remains scarce; thus, the evaluation of the ecological value of GPPs for floodplain wetland species is not sufficient. Species composition in floodplain landscapes often differs among waterbody types (Ishiyama et al., 2016), and the differences may contribute to the maintenance of gamma diversity. Therefore, we should assess community structures and abiotic characteristics of GPPs in floodplain landscapes by comparing them with other floodplain wetlands to deeply understand the contribution of GPPs to regional aquatic biodiversity.

Freshwater fishes suffer severely from several human activities, including agricultural activities, inland fisheries, habitat fragmentation, biological invasions, and climate change (Allan et al., 2005; Barbarossa et al., 2021; Dudgeon, 2019; Gallardo et al., 2016; Maitland, 1995; Reid et al., 2019; Weijters et al., 2009). Therefore, effective conservation measures for freshwater fish are needed. This study aimed to evaluate the ecological value of GPPs for floodplain wetland fish by comparing abiotic and biotic conditions among three types of waterbodies. In this paper, ecological value is defined as the capacity of a habitat to support an abundance and diversity of organisms. We selected two floodplain ponds, a "remnant pond" and a "river backwater", in addition to GPPs. Remnant ponds are permanent water bodies that include cut-off channels and remnants of the back marsh (Yamanaka et al., 2020). River backwaters are slow-flowing areas that are separated from the influence of the main channel (Moore & Gregory, 1988). We compared fish assemblages and environments among the three pond types based on the hypothesis that GPPs function as important habitats for fish communities, similar to other pond types, and contribute to an increase in gamma diversity in a region. We predicted that each of the three pond types would provide habitats for unique fish species due to their different environments (e.g., water temperatures and distance from the main channel).

2. MATERIALS AND METHODS

2.1 Study area

Field surveys were conducted in the Tokachi Plain, Hokkaido, northern Japan. Since 1900, this region has been undergoing agricultural land expansion and river channelization, and most of the wetlands have been converted to farmland. We randomly selected five study sites for each pond type (Figure 1). All study ponds are lentic and connected to main channels through waterways, although some ponds are connected to main channels only when the water level rises. The mean and range for the area of each pond type are as follows: GPPs, 4349.8 (range 247–10746) m^2; remnant ponds, 4837.8 (range 548–10197) m^2; and river backwaters, 396.6 (range 219–665) m^2.

2.2 Environmental factors

Abiotic surveys were conducted from July 20th to August 6th, 2021. All environmental measurements and fish surveys were conducted during the same season and completed within 30 days after the fish survey. We measured the dissolved oxygen content, electrical conductivity, turbidity, water temperature, and pH at three points randomly selected at each site using a portable water quality metre (WQC-24, DKK-TOA Corporation, Tokyo, Japan). These environmental factors were averaged for each pond for data analysis. These measurements were taken within 5 h after sunrise. We also measured water levels with a folding scale or a portable echosounder (Deeper Smart Sonar CHIRP$^+$, Deeper, Vilnius, Lithuania) at 20 points in each site, at 10 points on the shore and at 10 points in the centre of the water body, and then an average was calculated for each position (i.e., centre or shore). Distance from the main channel (excluding ditches) was measured as an indicator of connectivity using Google Maps (https://www.google.co.jp/maps/) for remnant ponds and GPPs and a laser rangefinder (Tru-Pulse 200, Laser Technology Inc., Colorado, US) for river backwaters.

2.3 Fish

From July 7th to August 5th, 2021, fish surveys were conducted using one fyke net (0.4 m diameter, 2.0 m bag length, and 3 m wing length) and two minnow traps (0.25 m width, 0.48 m length, and 0.25 m depth) at each site. The fyke net and minnow traps were set up near shores covered by aquatic vegetation for 24 h. The collected fish were anaesthetized with 2-phenoxyethanol and identified to the species level, and the abundance of each species was recorded. Then, all fish were released near the capture sites. The collected fish were also categorized into native or nonnative species according to the Hokkaido Blue List 2010 (Hokkaido, 2010), and the status of each fish species was assessed according to national red lists (Ministry of the Environment, 2020). The samples from fyke net and minnow traps were pooled in each pond for data analysis. Fish surveys were conducted at one or two ponds per day. The sampling effort needed to comprehensively capture that community structure can vary among study ponds. Prior to the statistical analyses, we compared the observed and estimated species richness within each pond using an individual-based rarefaction curve (Colwell et al., 2012) to test whether the community in each pond was well represented by the sampling data. The difference between the observed and estimated species richness within each pond was small (Figure S1; mean detection rate ± SD, 95 ± 8% [range 75–100%]). The result suggests that the sampling effort used in this study was appropriate for capturing the community structure.

2.4 Data analysis

Since candidate water bodies were very few and unevenly distributed spatially due to river regulation, river channelization, and conversion to agricultural land, our study sites for each of the pond types exhibited an aggregated pattern (Figure 1). Thus, we conducted a Moran's test to check for spatial autocorrelation of the abundance and species richness of native species among the study sites in each pond type. The results showed no significant correlations among sites and suggested that spatial autocorrelation does not occur in the present study design, and the samples can be treated as independent.

We constructed generalized linear models (GLMs) to estimate the effects of pond type on environmental factors, species richness and abundance. In the GLMs, we used environmental factors, species richness and abundance as response variables and pond type as an explanatory variable. Due to the fact that environmental factors were comprised of non-negative continuous data, species richness was comprised of non-overdispersed count data and abundance was comprised of overdispersed count data, we applied a gamma distribution with a log link function, a Poisson distribution with a log link function and a negative binominal distribution with a log link function in the GLMs, respectively (Zuur et al., 2009). In the GLMs with species richness or abundance as a response variable, native and nonnative species were used in separate models. Second, we conducted pairwise comparisons using the constructed models to examine whether each environmental factor, species richness, and abundance significantly differed among the pond types. *p*-values were corrected for pairwise comparisons using the Holm procedure (Holm, 1979).

To compare species composition among the pond types, we ordinated species composition by nonmetric multidimensional scaling (NMDS). A dataset including both native and nonnative species was used for this analysis. In the NMDS analysis, we used the log-transformed species-abundance data and Bray–Curtis index as the length index. We tested whether the environmental factors were significantly correlated with NMDS ordination with 1000 permutations. Before the analysis, we calculated the variance inflation factors (VIFs) to avoid multicollinearity; the results showed that depth near shore and depth in the centre had values over 5, which is the threshold indicative of problematic collinearity for regressions (Sheather, 2009). Therefore, we removed the depth in the centre, which had a lower R^2 than the depth near the shore, from our analysis. Finally, the VIF for every variable was <5, suggesting that all variables were suitable. Only environmental factors with significant correlation ($p < 0.05$) were fitted and plotted on the given NMDS using the "ordisurf" function of the "vegan" R package (Oksanen et al., 2020). We also conducted pairwise permutational multivariate analysis of variance (pairwise PERMANOVA) to test for differences in species composition among the pond types. *p*-values from pairwise PERMANOVA were corrected by using the Holm procedure (Holm, 1979). The dispersion among the pond types was similar, with no significant differences.

Furthermore, we used indicator species analysis to determine which species were significantly associated with a specific pond type (Dufrene & Legendre, 1997). Indicator species were determined based on significant *p*-values (< 0.05, which was computed by using 10,000 permutations).

All data analyses were conducted with R v. 4.2.0 (R Core Team, 2022) using "emmeans" v. 1.7.4.1 (Lenth, 2022) for pairwise comparisons, "iNEXT" v. 2.0.20 (Chao et al., 2014) for rarefaction curve construction, "stats" v. 4.2.0 (R Core Team, 2022) and "MASS" v. 7.3.56 (Venables & Ripley, 2002) for GLM fitting, "vegan" v. 2.6.2 (Oksanen et al., 2020) for NMDS, "pairwiseAdonis" v. 0.4 (Martinez Arbizu, 2017) for pairwise PERMANOVA and "indicspecies" v. 1.7.12 (Cáceres & Legendre, 2009) for indicator species analysis.

3. RESULTS

3.1 Environmental factors

Water temperature was lower in river backwaters than in other pond types (Figure 2e; Table S1; Table S2), and the distance from the main channel to river backwaters was shorter than that to other pond types (Figure 2f; Table S1; Table S2). Other environmental factors did not significantly differ among the pond types (Figure 2a–d, g, h; Table S1; Table S2).

3.2 Fish

We caught 12193 and 708 individuals representing 12 native and 4 nonnative species, respectively. Regarding red list species, *Rhynchocypris percnura sachalinensis* was mainly found in GPPs, *Gymnogobius castaneus* and *Pungitius tymensis* were found only in remnant ponds, *Lethenteron* sp. N (one of the two cryptic species of *Lethenteron reissneri*) and *Salvelinus curilus* were found only in river backwaters, and *Lefua nikkonis* was present in all pond types (Figure S2; Figure S3; Table S3). Additionally, one or two species were dominant in each pond type, i.e., *Gasterosteus aculeatus* in river backwaters (Figure S2; Figure S3; Table S3). There was no significant difference in species richness or abundance among the pond types except for the abundance of nonnative species (Figure 3a–c; Table S4; Table S5). The nonnative species abundance of remnant ponds was significantly greater than that of river backwaters (Figure 3d; Table S4; Table S5). Species composition significantly differed among the pond types (Figure 4a; Table 1). The stress value, which is an index of the fit of the reproduced similarity matrix to the observed similarity matrix, was 0.11, suggesting that the goodness of the fit was 'fair' (Kruskal, 1964). Turbidity, water temperature, distance from the main channel, and depth near shore were significantly correlated with NMDS ordination (Figure 4b–e; Table S6). While river backwaters and other pond types clearly separated along the water temperature gradient and differed in distance from the main channel (Figure 4c, d), no clear pattern was found in other factors. The indicator species analysis showed that one species was a significant indicator for each pond type (Table 2): GPPs, *Rhynchocypris percnura sachalinensis*; remnant ponds, *Carassius* sp. ; and river backwaters, *Lethenteron* sp. N.

4. DISCUSSION

The degradation of floodplains leads to a serious decline in the abundance of floodplain wetland species (Poff et al., 1997). In the present study, we clarified the ecological value of GPPs by comparing biotic and abiotic conditions among multiple pond types in modified floodplain landscapes. We found that species composition differed significantly among the pond types, although the richness and abundance of native species did not differ. Indicator species also differed among the pond types. These results support our hypothesis that GPPs function as important habitats for fish communities, similar to other pond types, and contribute to an increase in gamma diversity in a region. Thus, appropriate management of GPPs is important to conserve floodplain wetland biodiversity that is being lost.

It is possible that the unique fish communities in each pond type were formed by the occurrence of nonnative species and/or environmental factors. River backwaters have lower temperatures and shorter distances from the main channel than the other pond types, and these gradients explained the community structure of river backwaters.

The indicator species *Lethenteron* sp. N and several other species (*Salvelinus curilus* and *Oncorhynchus mykiss*) that were found only in river backwaters prefer spring water and/or cold water habitats (Hirano et al., 2020; Koizumi & Maekawa, 2004; Matthews & Berg, 1997). Therefore, the cold water in river backwaters may have caused the formation of a unique community. Also, river backwaters exhibited the lowest nonnative species abundance, which was significantly lower than that in remnant ponds. Invasion by lentic or low-flow nonnative species may be prevented by flood disturbance (Ho et al., 2013). Therefore, a high frequency of flood disturbance in river backwaters may cause a lower abundance of nonnative species.

Although GPPs and remnant ponds had more similar environments than we predicted, their species composition and indicator species differed as predicted. In GPPs, only one nonnative species (*Misgurnus anguillicaudatus*) was observed, although no significant differences in the richness or abundance of nonnative species were found between GPPs and remnant ponds. Since public access to the area near GPPs is prohibited, the release of nonnative species may have been prevented. *Rhynchocypris percnura sachalinensis* (categorized as near-threatened) was the indicator species in GPPs but not in remnant ponds with similar environments. The reason for this difference may be the effect of nonnative species. Invasion by nonnative *Pseudorasbora parva*, with an ecological niche similar to that of *Rhynchocypris percnura sachalinensis*, can reduce the abundance of *Rhynchocypris percnura sachalinensis* (Ishiyama et al., 2020). Since *Pseudorasbora parva* inhabited three remnant ponds, the abundance of *Rhynchocypris percnura sachalinensis* may have been low. In addition, deeper ponds probably function as refuges for *Rhynchocypris percnura sachalinensis* from *Pseudorasbora parva* (e.g., Ishiyama et al., 2020); therefore, deeper GPPs created by gravel mining may function as refuges for *Rhynchocypris percnura sachalinensis* if the nonnative *Pseudorasbora parva* invades.

Our results showed that GPPs provide habitats for floodplain wetland fishes, including endangered species, and can help increase the gamma diversity of wetland fishes in the studied region. Most species found in the studied ponds prefer lentic water and have a weak swimming ability (Ishiyama et al., 2014). Thus, if habitat fragmentation by river alteration proceeds, dispersion of wetland fishes may be limited, and populations may not be sustained. Conservation of existing GPPs may contribute to sustaining the habitat and populations of wetland fishes. However, the ecological value of GPPs has been overlooked, and GPPs are disappearing in Japan. For example, GPPs in some prefectures should be backfilled after mining projects due to past fatal water accidents. GPPs often have steeper shores than natural lakes or ponds (Blanchette & Lund, 2016; Emmrich et al., 2014; Santoul et al., 2004); however, this structure is not conducive to the growth of macrophytes (Søndergaard et al., 2018). Inshore macrophytes can serve as habitats for many organisms and increase overall biodiversity (Santoul et al., 2004). Therefore, creating gently sloping shores for GPPs may be a solution for biological conservation as well as the prevention of water accidents.

Our results indicated that GPPs have an important ecological role for floodplain wetland fishes and can compensate for wetland loss. Although our study focused only on floodplain wetland fishes, various types of organisms inhabit GPPs (including gravel pit lakes) (Emmrich et al., 2014; Santoul et al., 2009; Seelen et al., 2021; Søndergaard et al., 2018; Vucic et al., 2019; Zhao et al., 2016). Since ecological values often differ among taxa (e.g., Yamanaka et al., 2020), it is important to clarify the ecological value of GPPs for other floodplain wetland taxa in future studies.

ACKNOWLEDGMENTS

We thank the members of the Ecosystem Management Laboratory, who helped conduct the field survey and gave valuable comments. We also thank Y. Oppata at the Higashitaisetsu Museum for field support. The Hokkaido Government Tokachi General Subprefectural Bureau provided permission (no. 7) to perform fish collection. This work was funded by the Research Fund for the Ishikari and Tokachi Rivers provided by the Ministry of Land, Infrastructure, Transport, and Tourism of Japan.

AUTHOR CONTRIBUTION STATEMENT

Conceptualization: TY. Developing methods: HN, TY, NI. Conducting the research, data analysis, preparation figures & tables: HN, TY. Data interpretation, writing: HN, TY, NI, FN.

DATA AVAILABILITY STATEMENT

Data used in this study will be made available by the authors upon reasonable request.

CONFLICTS OF INTEREST STATEMENT

None declared.

REFERENCES

Allan, J. D., Abell, R., Hogan, Z., Revenga, C., Taylor, B. W., Welcomme, R. L., & Winemiller, K. (2005). Overfishing of inland waters. *BioScience*, *55*(12), 1041–1051. https://doi.org/10.1641/0006-3568(2005)055[1041:OOIW]2.0.CO;2

Barbarossa, V., Bosmans, J., Wanders, N., King, H., Bierkens, M. F. P., Huijbregts, M. A. J., & Schipper, A. M. (2021). Threats of global warming to the world's freshwater fishes. *Nature Communications*, 12(1). https://doi.org/10.1038/s41467-021-21655-w

Bendixen, M., Overeem, I., Rosing, M. T., Bjørk, A. A., Kjær, K. H., Kroon, A., … Iversen, L. L. (2019). Promises and perils of sand exploitation in Greenland. *Nature Sustainability*, *2*(2), 98–104. https://doi.org/10.1038/s41893-018-0218-6

Blanchette, M. L., & Lund, M. A. (2016). Pit lakes are a global legacy of mining: an integrated approach to achieving sustainable ecosystems and value for communities. *Current Opinion in Environmental Sustainability*, *23*, 28–34. https://doi.org/10.1016/j.cosust.2016.11.012

Cáceres, M. De, & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, *90*(12), 3566–3574. https://doi.org/10.1890/08-1823.1

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Chester, E. T., & Robson, B. J. (2013). Anthropogenic refuges for freshwater biodiversity: Their ecological characteristics and management. *Biological*

Conservation, *166*, 64–75. https://doi.org/10.1016/j.biocon.2013.06.016

Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S. Y., Mao, C. X., Chazdon, R. L., & Longino, J. T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, *5*(1), 3–21. https://doi.org/10.1093/jpe/rtr044

Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, *65*(10), 934–941. https://doi.org/10.1071/MF14173

Dudgeon, D. (2019). Multiple threats imperil freshwater biodiversity in the Anthropocene. *Current Biology*, *29*(19), R960–R967. https://doi.org/10.1016/j.cub.2019.08.002

Dufrene, M., & Legendre, P. (1997). Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. *Ecological Monographs*, *67*(3), 345. https://doi.org/10.2307/2963459

Emmrich, M., Schälicke, S., Hühn, D., Lewin, C., & Arlinghaus, R. (2014). No differences between littoral fish community structure of small natural and gravel pit lakes in the northern German lowlands. *Limnologica*, *46*, 84–93. https://doi.org/10.1016/j.limno.2013.12.005

Fickas, K. C., Cohen, W. B., & Yang, Z. (2016). Landsat-based monitoring of annual wetland change in the Willamette Valley of Oregon, USA from 1972 to 2012. *Wetlands Ecology and Management*, *24*(1), 73–92. https://doi.org/10.1007/s11273-015-9452-0

Gallardo, B., Clavero, M., Sánchez, M. I., & Vilà, M. (2016). Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology*, *22*(1), 151–

163. https://doi.org/10.1111/gcb.13004

Hein, T., Schwarz, U., Habersack, H., Nichersu, I., Preiner, S., Willby, N., & Weigelhofer, G. (2016). Current status and restoration options for floodplains along the Danube River. *Science of the Total Environment*, *543*, 778–790. https://doi.org/10.1016/j.scitotenv.2015.09.073

Hirano, Y., Kidera, N., Kondo, N. I., & Nishihiro, J. (2020). Habitat characteristics and size structure in a population of an endangered lamprey, *Lethenteron* sp. N, in an urbanized area of Japan. *Ichthyological Research*, *67*(4), 545–551. https://doi.org/10.1007/s10228-020-00747-5

Ho, S. S., Bond, N. R., & Thompson, R. M. (2013). Does seasonal flooding give a native species an edge over a global invader? *Freshwater Biology*, *58*(1), 159–170. https://doi.org/10.1111/fwb.12047

Hokkaido. (2010). Hokkaido Blue List 2010 (in Japanese). Retrieved May 10, 2022, from http://bluelist.pref.hokkaido.lg.jp

Holm, S. (1979). A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian Journal of Statistics*, *6*(2), 65–70.

Ishiyama, N., Akasaka, T., & Nakamura, F. (2014). Mobility-dependent response of aquatic animal species richness to a wetland network in an agricultural landscape. *Aquatic Sciences*, *76*(3), 437–449. https://doi.org/10.1007/s00027-014-0345-8

Ishiyama, N., Miura, K., Yamanaka, S., Negishi, J. N., & Nakamura, F. (2020). Contribution of small isolated habitats in creating refuges from biological invasions along a geomorphological gradient of floodplain waterbodies. *Journal of Applied Ecology*, *57*(3), 548–558. https://doi.org/10.1111/1365-2664.13546

Ishiyama, N., Sueyoshi, M., Watanabe, N., & Nakamura, F. (2016). Biodiversity and rarity distributions of native freshwater fish in an agricultural landscape: the importance of β diversity between and within water-body types. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(3), 416–428. https://doi.org/10.1002/aqc.2583

Ishiyama, N., Yamanaka, S., Ooue, K., Senzaki, M., Kitazawa, M., Morimoto, J., & Nakamura, F. (2022). Flood-Control Basins as Green Infrastructures: Flood-Risk Reduction, Biodiversity Conservation, and Sustainable Management in Japan. In F. Nakamura (Ed.), *Green Infrastructure and Climate Change Adaptation* (pp. 189–207). Singapore: Springer. https://doi.org/10.1007/978-981-16-6791-6_12

Keddy, P. A., Fraser, L. H., Solomeshch, A. I., Junk, W. J., Campbell, D. R., Arroyo, M. T. K., & Alho, C. J. R. (2009). Wet and wonderful: the world's largest wetlands are conservation priorities. *BioScience*, *59*(1), 39–51. https://doi.org/10.1525/bio.2009.59.1.8

Kingsford, R. T. (2000). Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology*, *25*(2), 109–127. https://doi.org/10.1046/j.1442-9993.2000.01036.x

Kingsford, R. T. (2015). Conservation of floodplain wetlands - out of sight, out of mind? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*(6), 727–732. https://doi.org/10.1002/aqc.2610

Kingsford, R. T., Basset, A., & Jackson, L. (2016). Wetlands: conservation's poor cousins. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(5), 892–916. https://doi.org/10.1002/aqc.2709

Koizumi, I., & Maekawa, K. (2004). Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. *Freshwater Biology*, *49*(8), 973–981. https://doi.org/10.1111/j.1365-2427.2004.01240.x

Kruskal, J. B. (1964). Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, *29*(1), 1–27. https://doi.org/10.1007/BF02289565

Kuiper, J. J., Janse, J. H., Teurlincx, S., Verhoeven, J. T. A., & Alkemade, R. (2014). The impact of river regulation on the biodiversity intactness of floodplain wetlands. *Wetlands Ecology and Management*, *22*(6), 647–658. https://doi.org/10.1007/s11273-014-9360-8

Lenth, R. V. (2022). *emmeans: Estimated Marginal Means, aka Least-Squares Means*.

Maitland, P. S. (1995). The conservation of freshwater fish: Past and present experience. *Biological Conservation*, *72*(2), 259–270. https://doi.org/10.1016/0006-3207(94)00088-8

Martinez Arbizu, P. (2017). *pairwiseAdonis: Pairwise Multilevel Comparison using Adonis*.

Matthews, K. R., & Berg, N. H. (1997). Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. *Journal of Fish Biology*, *50*(1), 50–67. https://doi.org/10.1111/j.1095-8649.1997.tb01339.x

Ministry of the Environment. (2020). Red List 2020 (in Japanese). Retrieved May 10, 2022, from http://www.env.go.jp/press/files/jp/114457.pdf

Mollema, P. N., & Antonellini, M. (2016). Water and (bio)chemical cycling in gravel pit lakes: A review and outlook. *Earth-Science Reviews*, *159*, 247–270. https://doi.org/10.1016/j.earscirev.2016.05.006

Moore, K. M. S., & Gregory, S. V. (1988). Response of Young-of-the-Year Cutthroat

Trout to Manipulation of Habitat Structure in a Small Stream. *Transactions of the American Fisheries Society*, *117*(2), 162–170. https://doi.org/10.1577/1548-8659(1988)117<0162:royoty>2.3.co;2

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2020). *vegan: Community Ecology Package*.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., … Stromberg, J. C. (1997). The Natural Flow Regime. *BioScience*, *47*(11), 769–784. https://doi.org/10.2307/1313099

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. Vienna, Austria. Retrieved from https://www.r-project.org/

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., … Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*(3), 849–873. https://doi.org/10.1111/brv.12480

Reis, V., Hermoso, V., Hamilton, S. K., Ward, D., Fluet-Chouinard, E., Lehner, B., & Linke, S. (2017). A Global Assessment of Inland Wetland Conservation Status. *BioScience*, *67*(6), 523–533. https://doi.org/10.1093/biosci/bix045

Santoul, F., Figuerola, J., & Green, A. J. (2004). Importance of gravel pits for the conservation of waterbirds in the Garonne river floodplain (southwest France). *Biodiversity and Conservation*, *13*(6), 1231–1243. https://doi.org/10.1023/B:BIOC.0000018154.02096.4b

Santoul, F., Gaujard, A., Angélibert, S., Mastrorillo, S., & Céréghino, R. (2009). Gravel pits support waterbird diversity in an urban landscape. *Hydrobiologia*, *634*(1), 107–114. https://doi.org/10.1007/s10750-009-9886-6

Seelen, L. M. S., Teurlincx, S., Bruinsma, J., Huijsmans, T. M. F., van Donk, E., Lürling, M., & de Senerpont Domis, L. N. (2021). The value of novel ecosystems: Disclosing the ecological quality of quarry lakes. *Science of the Total Environment*, *769*. https://doi.org/10.1016/j.scitotenv.2020.144294

Sheather, S. (2009). A Modern Approach to Regression with R. In *Journal of Statistical Software*. New York, NY: Springer New York. https://doi.org/10.1007/978-0-387-09608-7

Søndergaard, M., Lauridsen, T. L., Johansson, L. S., & Jeppesen, E. (2018). Gravel pit lakes in Denmark: Chemical and biological state. *Science of the Total Environment*, *612*, 9–17. https://doi.org/10.1016/j.scitotenv.2017.08.163

Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: Present state and future trends. *Environmental Conservation*, *29*(3), 308–330. https://doi.org/10.1017/S037689290200022X

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S*. New York: Springer New York. https://doi.org/10.1007/978-0-387-21706-2

Vucic, J. M., Cohen, R. S., Gray, D. K., Murdoch, A. D., Shuvo, A., & Sharma, S. (2019). Young gravel-pit lakes along Canada’s Dempster Highway: How do they compare with natural lakes? *Arctic, Antarctic, and Alpine Research*, *51*(1), 25–39. https://doi.org/10.1080/15230430.2019.1565854

Weijters, M. J., Janse, J. H., Alkemade, R., & Verhoeven, J. T. A. (2009). Quantifying the effect of catchment land use and water nutrient concentrations on freshwater river and stream biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*(1), 104–112. https://doi.org/10.1002/aqc.989

Wilcock, D. N., & Essery, C. I. (1991). Environmental impacts of channelization on the river main, County Antrim, Northern Ireland. *Journal of Environmental Management*, *32*(2), 127–143. https://doi.org/10.1016/S0301-4797(05)80029-5

Yamanaka, S., Ishiyama, N., Senzaki, M., Morimoto, J., Kitazawa, M., Fuke, N., & Nakamura, F. (2020). Role of flood-control basins as summer habitat for wetland species - A multiple-taxon approach. *Ecological Engineering*, *142*, 105617. https://doi.org/10.1016/j.ecoleng.2019.105617

Zhao, T., Grenouillet, G., Pool, T., Tudesque, L., & Cucherousset, J. (2016). Environmental determinants of fish community structure in gravel pit lakes. *Ecology of Freshwater Fish*, *25*(3), 412–421. https://doi.org/10.1111/eff.12222

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer New York. https://doi.org/10.1007/978-0-387-87458-6

TABLES

Table 1 Results of pairwise PERMANOVA.

Contrast	***F***	***p***
Gravel pit pond vs. Remnant pond	2.31	< 0.05
Gravel pit pond vs. River backwater	6.49	< 0.05
Remnant pond vs. River backwater	4.81	< 0.05

Table 2 Results of the indicator species analysis. Specificity is the probability that the surveyed site belongs to the target site group given that the species has been found. Sensitivity is the probability of finding the species in sites belonging to the site group. Only species with $p < 0.05$ are shown.

Pond type	**Species**	**Specificity**	**Sensitivity**	***p***
Gravel pit pond	*Rhynchocypris percnura sachalinensis*	0.96	1.00	< 0.01
Remnant pond	*Carassius* sp.	0.82	0.80	< 0.05
River backwater	*Lethenteron* sp. N	1.00	0.80	< 0.01

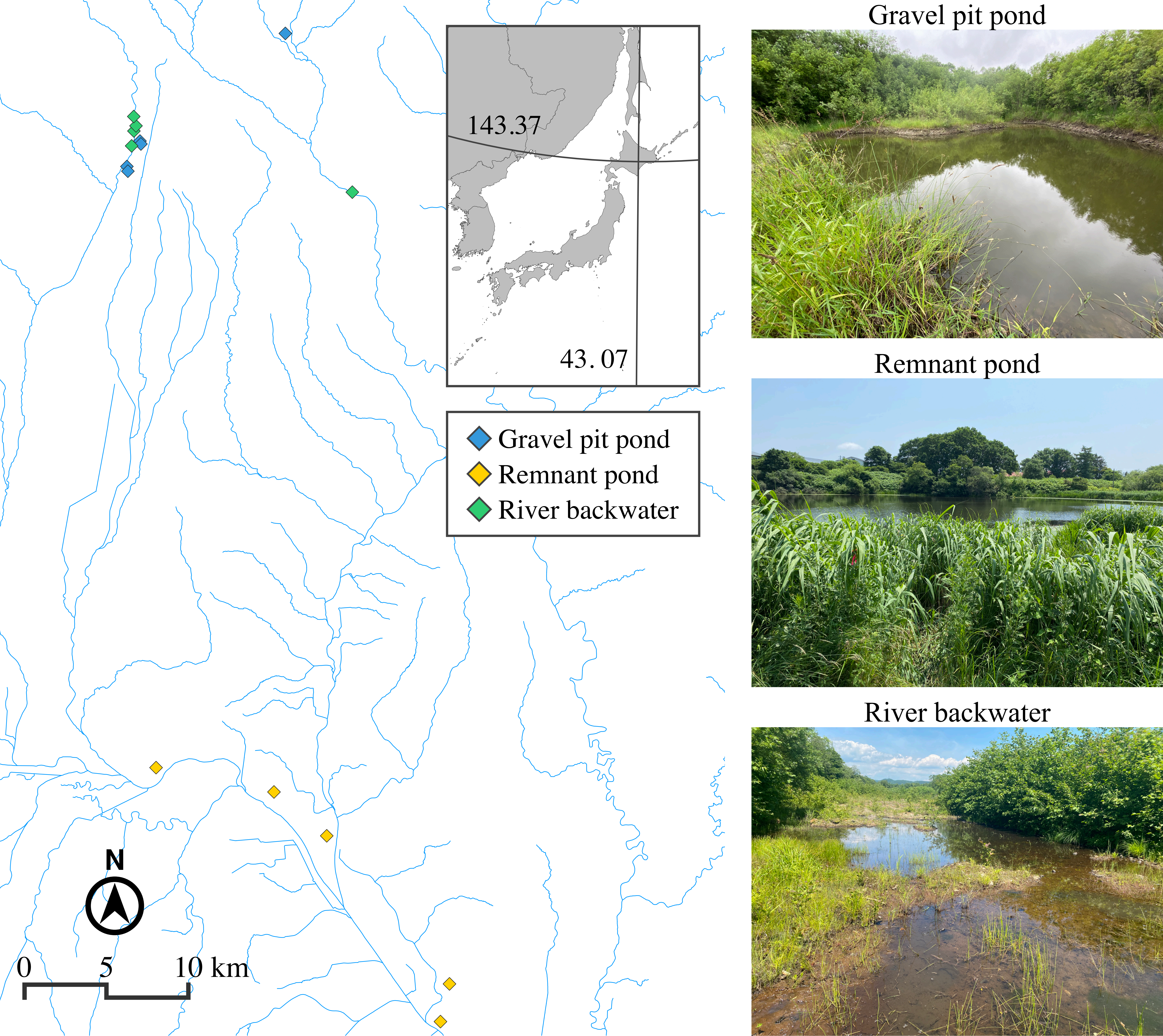
FIGURE CAPTIONS

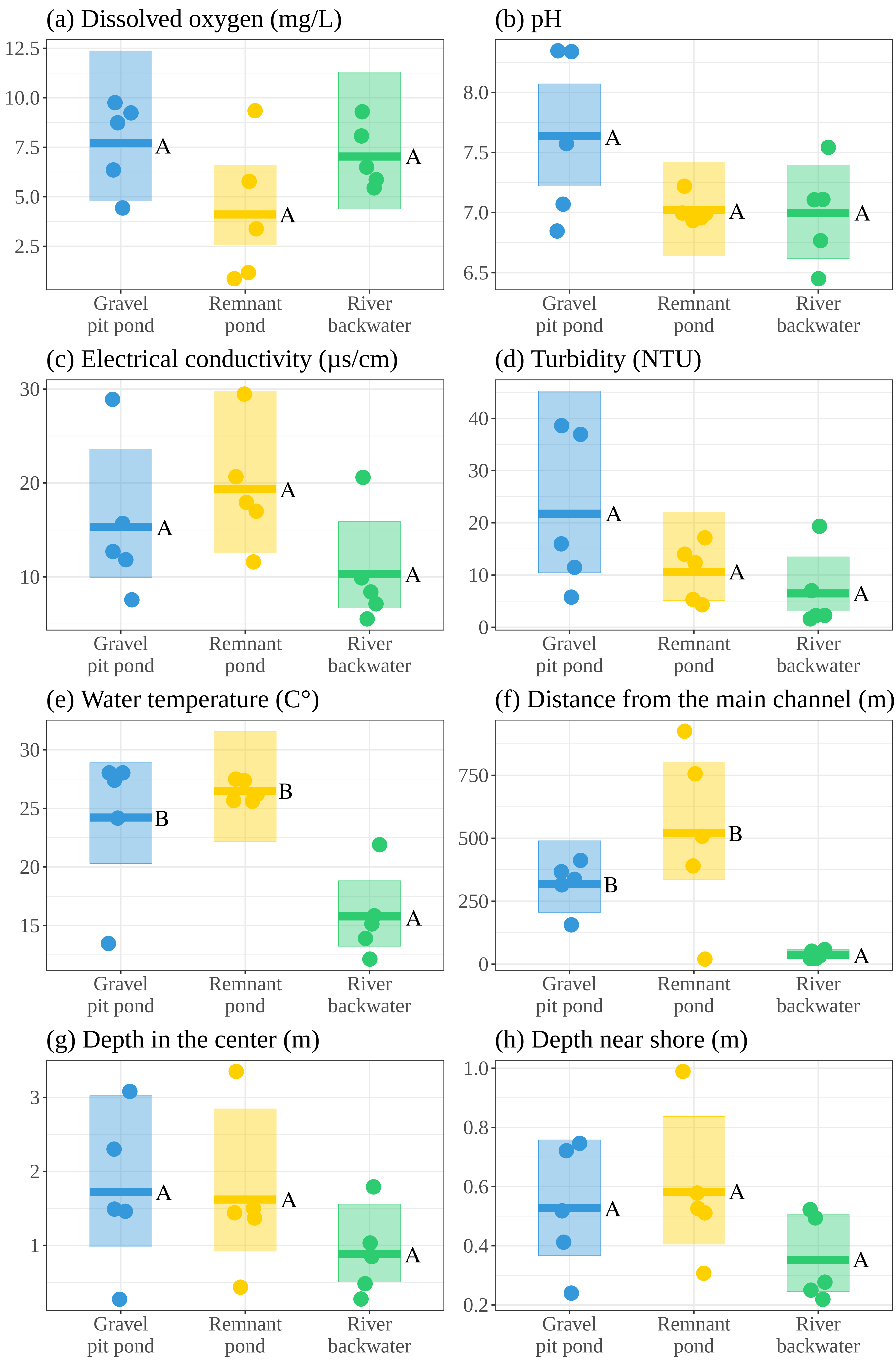
Figure 1 Map of the study area and representative landscapes of the surveyed ponds.

Figure 2 Differences in environmental factors among the pond types. The translucent bars indicate 95% CIs. The circles denote each observed value. Different letters indicate significant differences in the pairwise comparison ($p < 0.05$).

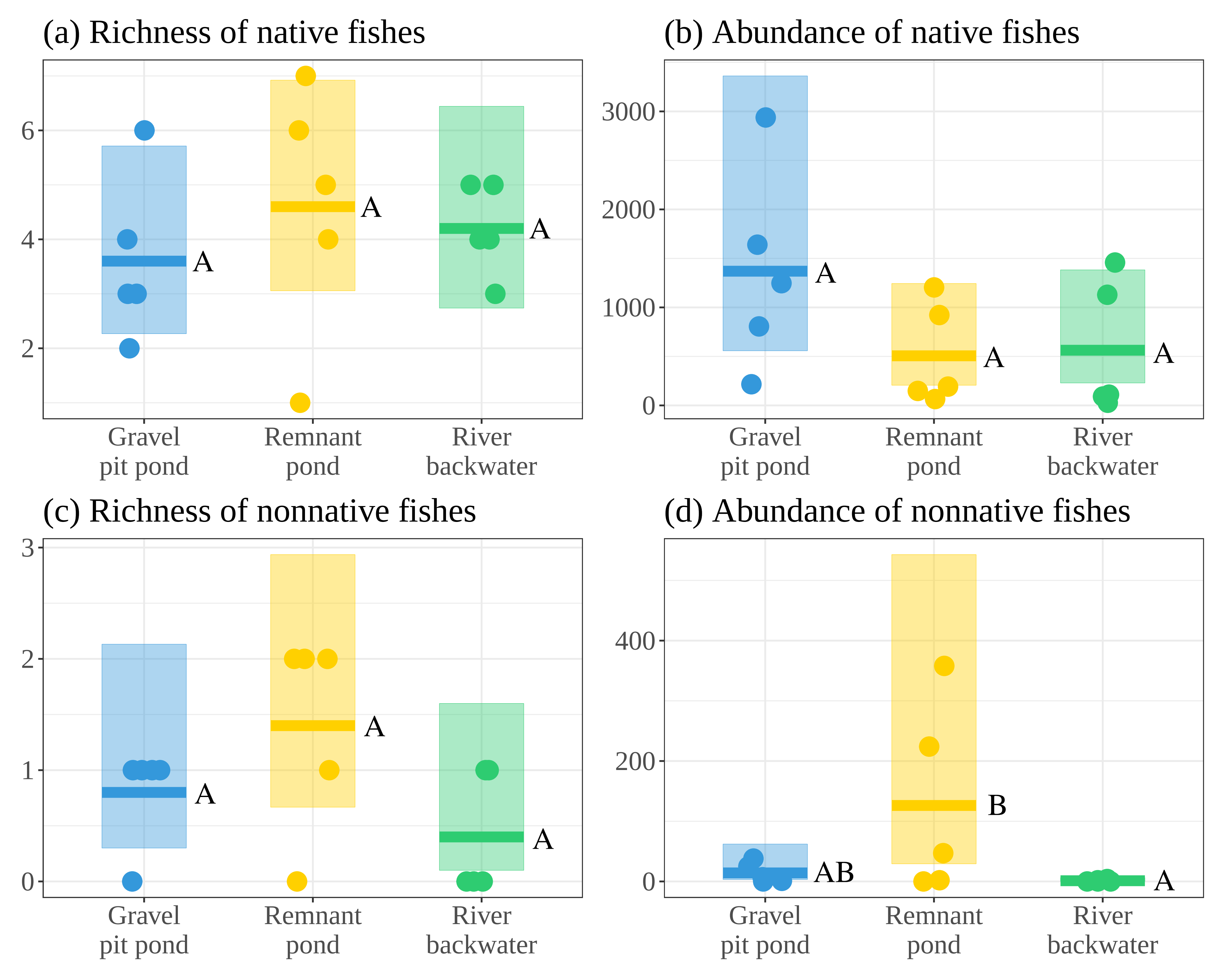
Figure 3 Differences in species richness and abundance among pond types. The translucent bars indicate 95% CIs. The circles denote each observed value. Different letters indicate significant differences in the pairwise comparison ($p < 0.05$).

Figure 4 Nonmetric multidimensional scaling (NMDS) of the fish community structures in the surveyed pond types. (a) Site scores coded by pond types. (b-f) Contour plots for each environmental factor. Greyscale bars in each panel indicate the range of values for each environmental factor.

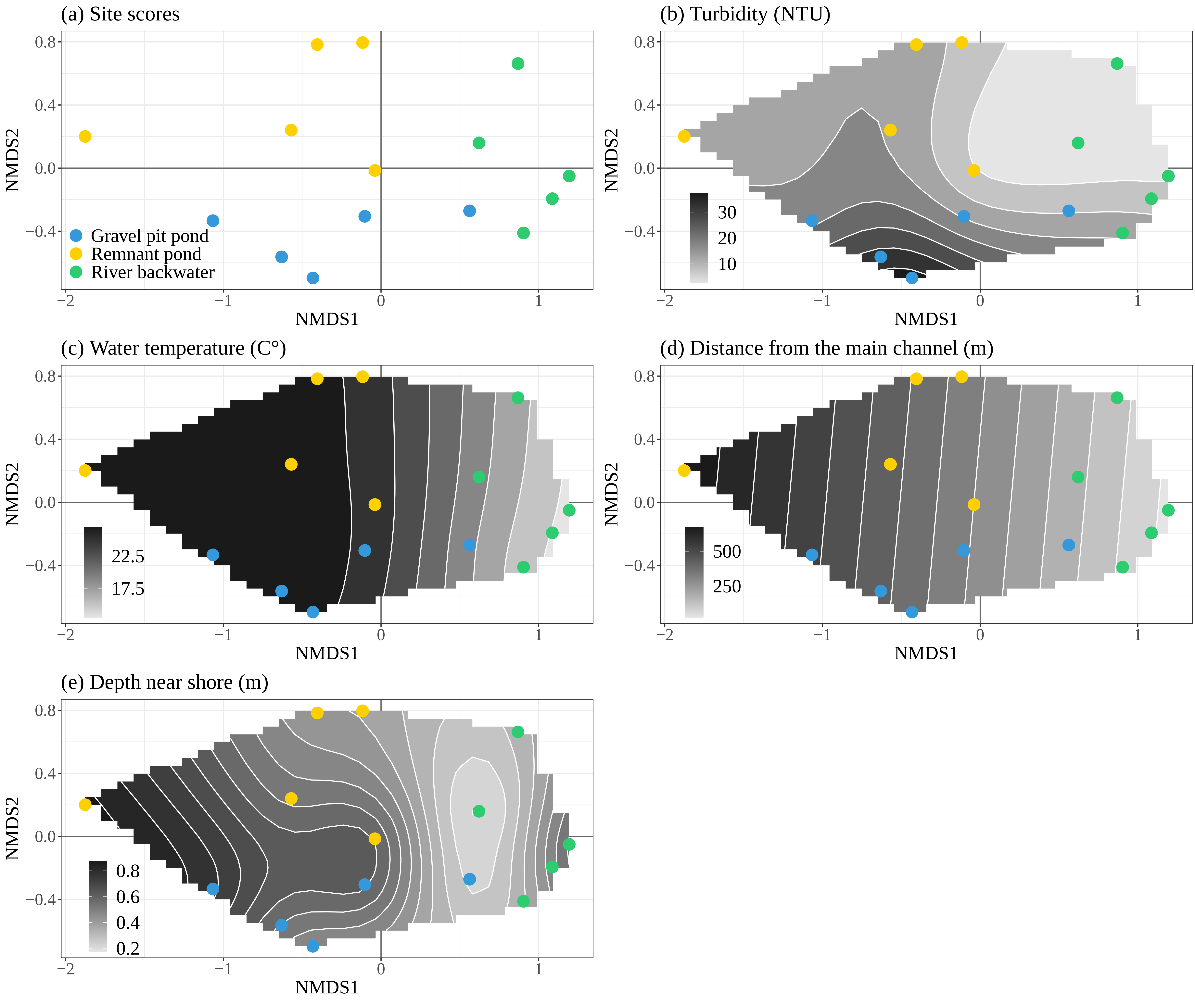

143.37
43.07
Gravel pit pond
Remnant pond
River backwater
N
0
5
10 km
Gravel pit pond
Remnant pond
River backwater



(a) Dissolved oxygen (mg/L)
(b) pH
(c) Electrical conductivity (µs/cm)
(d) Turbidity (NTU)
(e) Water temperature (C°)
(f) Distance from the main channel (m)
(g) Depth in the center (m)
(h) Depth near shore (m)
Gravel pit pond
Remnant pond
River backwater
A
B



(a) Richness of native fishes
6
4
2
A
A
A
Gravel pit pond
Remnant pond
River backwater
(b) Abundance of native fishes
3000
2000
1000
0
A
A
A
Gravel pit pond
Remnant pond
River backwater
(c) Richness of nonnative fishes
3
2
1
0
A
A
A
Gravel pit pond
Remnant pond
River backwater
(d) Abundance of nonnative fishes
400
200
0
AB
B
A
Gravel pit pond
Remnant pond
River backwater



(a) Site scores
Gravel pit pond
Remnant pond
River backwater
(b) Turbidity (NTU)
30
20
10
(c) Water temperature (C°)
22.5
17.5
(d) Distance from the main channel (m)
500
250
(e) Depth near shore (m)
0.8
0.6
0.4
0.2
NMDS1
NMDS2
0.8
0.4
0.0
−0.4
−2
−1
0
1