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Effects of land use on trophic states and multi-taxonomic diversity in Japanese farm ponds

Nisikawa Usio [a,*] Megumi Nakagawa [b], Takashi Aoki [c], Shinsuke Higuchi [d], Yasuro Kadono [d], Munemitsu Akasaka [e] and Noriko Takamura [b]

[a] *Institute of Nature and Environmental Technology, Kanazawa University, Kanazawa 920-1192, Japan*

[b] *Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies, Tsukuba 305-8506, Japan*

[c] *Suma-shofu High School, Kobe 654-0155, Japan (Present address: Fujimiga-oka 2-19-13, Nishi-ku, Kobe 651-2214, Japan)*

[d] *Graduate School of Science, Kobe University, Kobe 657-8501, Japan*

[e] *Tokyo University of Agriculture and Technology, Tokyo 183-8509, Japan*

* *Correspondence author at: Institute of Nature and Environmental Technology, Kanazawa University, Kanazawa 920-1192, Japan*

E-Mail: usio@se.kanazawa-u.ac.jp (Nisikawa Usio)

Abstract

Farm ponds are among the most biodiverse anthropogenic freshwater habitats because of their small size, shallow water depth, and aquatic vegetation. Land-use changes, such as converting riparian vegetation to human use or changing the management practices of farm ponds, are assumed to be major factors that change such ecosystems from a clear-water state to a turbid state, leading to deterioration of water quality and biodiversity in such ponds. Using the database of a large-scale pond survey, we evaluated the effects of surrounding land use (landscape factors and modern pond management practices), fish abundance, and other environmental variables on total phosphorus concentration and taxonomic richness patterns of six biological indicators associated with changes in the trophic state. Local- and landscape-level vegetation structure associated with land use and total fish abundance were among the factors influencing the total phosphorus concentration of farm ponds, a main driver of trophic state changes. In addition, a transition from a clear-water state to a turbid state was associated with lower taxonomic richness of aquatic plants, macroinvertebrates, and adult Odonata, and a higher taxonomic richness of phytoplankton and fish. Based on these results, we discuss potential land-use and pond management strategies for conserving and/or restoring the water quality and biodiversity of farm ponds through maintenance of a clear-water state.

Keywords: Biodiversity, Agricultural pond, Stable state, Alpha diversity, Satoyama

1. Introduction

Land-use changes, such as conversion of natural vegetation to farmland or residential areas and changing traditional management practices of secondary nature, have bi-directional consequences for the environment and human society. On the one hand, some land-use practices, such as creation of farmland or urbanisation, are essential to meet the increasing demand for food and/or space for human society. On the other hand, such practices have detrimental impacts on biodiversity and ecosystem functions and thereby affect the ecosystem services upon which human society depends. It is widely acknowledged that solely conserving or restoring biodiversity and ecosystem services in protected areas is insufficient for sustainable conservation and use of natural resources (Lundholm and Richardson, 2010; Chester and Robson, 2013). For the purpose of reconciling biodiversity conservation and human use of natural resources, management of human-altered landscapes is important (Rosenzweig, 2003; Dudgeon *et al.*, 2006).

Despite the common view that anthropogenic ecosystems have low levels of biodiversity, recent studies have shown that water bodies in agricultural and urban landscapes, such as farm ponds, highway ponds, paddy fields, and irrigation ditches, play important roles in biodiversity conservation (Elphick, 2000; Cereghino *et al.*, 2008; Le Viol *et al.*, 2009; Negishi *et al.*, 2014; Wezel *et al.*, 2014). Farm ponds in particular have been shown to be among the most biodiverse water bodies because of their small size, shallow water depth, and aquatic vegetation (Williams *et al.*, 2004; Davies *et al.*, 2008). Developing strategies to manage the multiple functions of anthropogenic freshwater ecosystems beyond their roles of irrigating, cropping, or controlling storm water is a key challenge in conservation science.

In Japan, most natural floodplain wetlands in lowland areas have been converted into agricultural or urban areas. Although farm ponds are created primarily for irrigation purposes to meet the increasing demand for food, these ponds serve as refuge habitats for aquatic and semi-aquatic wildlife that once inhabited natural floodplain wetlands. In practice, farm ponds contain many indigenous or endangered species that are absent from natural wetland habitats (Takamura, 2012). However, biodiversity in farm ponds is threatened because of increased demands for land consolidation and changes in management styles of ponds over time.

Farm ponds have alternative stable states characterised by different trophic states: a clear-water state and a turbid state (Declerck *et al.*, 2006; Phillips *et al.*, 2016). Previous studies have reported that changes from a clear-water state to a turbid state in shallow lakes or ponds are caused by various abiotic and biotic stresses. For example, non-point source pollution from farmland and urban areas is a major factor that enhances nutrient input into shallow lentic systems (Carpenter *et al.*, 1998). Land-use changes, such as deforestation in the surrounding area and input of agrochemicals through agricultural intensification, have been reported to deteriorate water quality and reduce the species richness of aquatic plants in farm ponds (Akasaka *et al.*, 2010). Ecosystem engineering via bioturbation activities by fish or macrophyte cutting and destruction by non-native crayfish are among the major factors that cause macrophyte reduction (Rodriguez *et al.*, 2005; Matsuzaki *et al.*, 2007; Scheffer and van Nes, 2007). Furthermore, fish predation on zooplankton can have positive effects on phytoplankton via trophic cascades (Vanni *et al.*, 1997). In most cases, such abiotic and biotic stresses are associated with trophic state changes via increased concentration of phosphorus and/or nitrogen (Jeppesen *et al.*, 1997; Declerck *et al.*, 2006)

Although our understanding of how multi-taxonomic groups respond to eutrophication is growing (Menetrey *et al.*, 2005; De Marco *et al.*, 2014; Rosset *et al.*, 2014; Wezel *et al.*, 2014), most researchers have directly addressed the response of biological indicators along the gradient of eutrophication and have not considered the relative effects of local and landscape factors on multi-taxonomic diversity. Furthermore, studies reporting the relative effects of local and landscape stressors on farm pond biodiversity are often limited to a restricted set of taxonomic groups such as aquatic plants (Akasaka *et al.*, 2010).

Using a database of 64 farm ponds with different land uses in western Japan (Takamura, 2011), we investigated the effects of surrounding landscape components, modern pond management practices, fish abundance, and other environmental variables on the trophic state of farm ponds to identify the major stressors of trophic state changes in such ponds. We hypothesised that local and landscape-level land uses, fish abundance, and the occurrence of invasive crayfish are significant stressors of trophic state changes. We subsequently documented the influence of changes in the trophic state on the taxonomic richness of phytoplankton, aquatic plants, zooplankton, macroinvertebrates, fish, and adult odonates in farm ponds. Given that aquatic plants provide refuge as well as foraging and/or spawning sites for many animals, and play vital roles in maintaining the clear-water state through various ecosystem functions (Jeppesen, 1998), we hypothesised that the taxonomic richness of aquatic plants and animals is positively associated with the clear-water state, while that of phytoplankton is negatively associated with such a state due to their counteracting association with aquatic plants (Phillips *et al.*, 2016). However, we expect that responses of taxonomic groups along the gradient of trophic states may be weak when the effects of other local and landscape stressors are simultaneously considered.

2. Methods

2.1. Study site

We used a database of biota (phytoplankton, aquatic plants, zooplankton, benthic macroinvertebrates, adult odonates, invasive animals, and floating-leaved macrophyte coverage), water quality, morphometric variables, landscape variables, and pond management at 64 farm ponds in the Kako River Basin of Hyogo Prefecture in western Japan (Takamura, 2011) (Figure 1, Table 1). Land-use variables consisted of both landscape variables (coverage of broadleaved forests, paddy fields, cropland, grassland, urban area, and freshwater within six multi-scale buffers ranging from 10 m to 2,000 m in radius) and modern pond management (coverage of concrete bank protection) (see below). Although the detailed history of each farm pond is unknown, most farm ponds in this region were created in the 19th century for the purposes of providing irrigation water to rice paddy fields.

We initially classified the farm ponds in the region on the basis of dominant land use (broadleaved forest, paddy fields, and urban area). For each land-use category, we subsequently selected three types of farm ponds on the basis of the aquatic vegetation characteristics (no vegetation, emergent macrophytes, and floating-leaved macrophytes). We arbitrarily selected seven to eight farm ponds from each of nine land use–aquatic vegetation categories. The 64 study ponds were generally small and shallow, with a mean surface area of 1.10 ha ± 1.48 (SD) (range 0.08–11.43 ha) and mean maximum water depth of 1.7 m ± 1.1 (SD) (range 0.1–4.8 m) (Table 1). The average total phosphorus concentration was 0.131 mg L^{-1} ± 0.140 (SD) (range 0.01–0.68 mg L^{-1}), and the total nitrogen concentration was 1.32 mg L^{-1} ± 1.30 (SD) (range 0.20–5.61 mg L^{-1}) in mid-summer (August).

2.2. Pond surveys

From April through November of 2006 and 2008, we sampled the farm ponds to assess water quality and taxonomic richness of phytoplankton, aquatic plants, zooplankton, macroinvertebrates, fish, and adult odonates. We used the six taxonomic groups as biological indicators because these groups are major components of farm pond communities and/or are generally taxon rich, and they are therefore suitable for bio-assessment based on taxonomic richness patterns. For phytoplankton, zooplankton, and water-quality samples, we performed a rapid assessment (without subsamples) at the 64 ponds over a relatively short period (7 days) in a single year to minimise temporal variation. For other biological indicators, we performed surveys over 2 or 3 years for logistical reasons. We also surveyed the occurrence (presence or absence) of two widely-distributed invasive species that can affect the water quality and taxonomic richness of biological indicators (see below). We performed a water-quality survey when nutrient concentrations would likely be highest (i.e. warmest month). For biological variables, we made sure to include the seasons when each taxonomic group would likely be at its highest abundance based on past experience with farm pond systems.

2.2.1. Water quality

From 23 to 29 August 2007, when cyanobacteria blooms were observed in some eutrophic farm ponds, we measured the water transparency (Secchi depth) and concentrations of chlorophyll-a, total phosphorus, total nitrogen, cyanobacteria, suspended solids, and bottom dissolved oxygen of each pond. At each farm pond, we took one measurement or sample for each water quality variable. We measured the concentration of cyanobacteria 20 cm below the water surface using a multiparameter water-quality sonde (YSI6600; YSI, Yellow Spring, Ohio) and dissolved oxygen immediately above the pond bottom using a dissolved oxygen meter (YSI58; YSI). By analysing a 2 L sample of surface water collected from each pond, we determined in the laboratory the concentration of total phosphorus by the ascorbic acid method (APHA, 1998), total nitrogen by the persulfate digestion method (APHA, 1998), suspended solids by drying (103°C for 1 h) and combusting (550°C for 1 h) duplicate filtered subsamples, and chlorophyll-a using a spectrophotometric method after extraction in 99% methanol (Marker *et al.*, 1980).

2.2.2. Phytoplankton

From 23 to 29 August 2007, we collected a water sample from 20 cm below the water surface of the deepest part of each pond using a 100-mL plastic bottle. At each farm pond, we took one water-phytoplankton sample. Following collection of each sample, we added several drops of Lugol's solution for sample preservation. In the laboratory, we used the sedimentation procedure (Utermöhl, 1958) to identify phytoplankton (mostly to the species level except for unidentifiable taxa) with the aid of an inverted microscope (400×). At each farm pond, we calculated total number of taxa as a measure of the taxonomic richness of phytoplankton.

2.2.3. Aquatic plants

From August to September 2006 and 2007, we recorded the occurrence of free-floating macrophytes, floating-leaved macrophytes, emergent macrophytes, and submerged macrophytes including charophytes in the study ponds while walking along the perimeter of the ponds. For deeper parts, we took a floater or boat out onto ponds and raked or lobbed a grapnel (a rake-like device mounted on a rope) on the pond bottom. Aquatic plants were identified mainly to the species level. At each farm pond, we calculated the total taxonomic richness of aquatic plants based on the one-time summer survey.

2.2.4. Zooplankton

From 23 to 29 August 2007, we used a plankton net (diameter 30 cm, length 70 cm, mesh size 25 μm) to perform a vertical net sweep 10 cm above the pond bottom at the centre of each pond. At each farm pond, we took one zooplankton sample. Samples were preserved in 1% neutral buffered formalin (APHA, 1998) and transported to the laboratory for microscopic analyses. In the laboratory, we identified zooplankton with the aid of inverted and binocular microscopes (40–200×). We counted at least 100 individuals for Copepoda, Podocopida and Rotifer, respectively. The zooplankton samples were identified mainly to species level; when species identification was not possible, such samples were identified to next possible taxonomic level (genus, family, etc.). At each farm pond, we calculated the total taxonomic richness of zooplankton.

2.2.5. Macroinvertebrates

In May of 2006 and 2007, we performed 3–12 horizontal net sweeps of 50 cm using a D-framed net (width 30 cm, length 30 cm, mesh size 200 μm) in the vegetated areas of the pond perimeter. We performed stratified sampling with three subsamples taken from each of up to four habitat types. In addition, we collected three Ekman grab samples (15 × 15 cm) from haphazardly selected points in the central area of each pond. We preserved the macroinvertebrate-sediment mixture in 10% formalin and transported the samples to an environmental consultant company (Chiiki Kankyo Keikaku, Takatsuki, Japan) for identification to the lowest possible taxonomic unit (mainly to the genus level). At each pond, we calculated macroinvertebrate taxonomic richness using combined data from the sweep and Ekman grab samples.

2.2.6. Fish and invasive species

From August to September 2006 and 2007, we sampled fish and decapod crustaceans by setting two fixed fishing nets (width 600 cm, length 304 cm, openings 69 cm, mesh size 4 cm) overnight along the perimeter of each pond and five baited (dried squid and fish sausages) box-shaped minnow traps (25 × 25 cm, length 40 cm, openings 6 cm, mesh size 2 mm) overnight at points equally spaced along the long axis of each pond. The following morning, we identified the animals in the nets and traps. We captured fish, decapod crustaceans, amphibians, and reptiles. In the present paper, however, we consider the data only for fish and the red swamp crayfish (*Procambarus clarkii*). We did not include amphibians in the analyses because no indigenous amphibian species were captured, probably because the survey was not performed when most indigenous amphibians spawn (early spring). We also excluded reptiles (turtles) from the analyses because the only indigenous turtle species (*Mauremys japonica*) was rare (occurred in only 4 of 64 sites) in the study ponds. At each farm pond, we calculated the total taxonomic richness and abundance (catch per unit effort) of fish using combined data from the fixed-net fishing and trapping.

Bluegill (*Lepomis macrochirus*) and red swamp crayfish were widely distributed non-native invasive species in the study area (Usio *et al.*, 2009). We determined the presence or absence of bluegill and red swamp crayfish using data from the fixed-net fishing, trapping, dip netting, and Ekman grab sampling.

2.2.7. Adult odonates

At each pond, we surveyed adult odonates between April and November (with the exception of August) of 2006 and 2008, for a total of six times. On average, we surveyed each pond for 22 min (± 14 SD) while walking the accessible parts of the pond perimeter or paddling along the pond margin. To avoid misidentification, we recorded sighted adult odonates using a video camera (DCR-HC96, SONY Inc., Japan). We identified most adult dragonflies to the species level by sight and later confirmed using the video recordings. For damselflies and Gomphidae, we identified individuals from samples collected using a sweep net or from the video recordings. In the subsequent statistical model, we used the total number of adult odonate species found at each farm pond during the six surveys.

2.3. Landscape variables

For each farm pond, we used ArcGIS version 9.1 (ESRI, Redlands, California) to calculate the coverage (proportions) of broadleaved forests, paddy fields, cropland, grassland, urban area, and freshwater within six multi-scale buffers ranging from 10 m to 2,000 m in radius (i.e. 10, 100, 250, 500, 1000, 2000 m). We created buffers from the edge of each farm pond that had a shape identical to that of the pond. Within these buffers, we calculated the coverage of each landscape factor using a land-use map (scale: 1:25,000) of the Japan Integrated Biodiversity Information System (Ministry of the Environment, 2000).

2.4. Pond management

Concrete bank construction is a typical, modern pond management practice in Japanese farm ponds that is implemented to avoid bank erosion and save labour for grass mowing. Using city planning maps (scale: 1:2,500) and ArcGIS, we calculated the proportion of concrete bank construction at each farm pond.

In contrast, pond draining is a traditional pond management practice that is performed to improve water quality or conduct social events, such as fish catching and barbequing. Through telephone interviews or direct communication with pond managers, we asked whether farm ponds had been drained prior to our field survey. Based on the interviews, we categorised ponds as drained (showing cracked earth at the bottom), partially drained (retaining water throughout the draining season), or undrained. We also asked the pond managers to provide the main water source for farm ponds. We categorised the source of water as agricultural drainage, dam water, or natural water (creek, underground, and/or rain water).

2.5. Data analysis

We used principal component analysis (PCA) on correlation matrices to reduce the seven highly correlated water-quality variables (chlorophyll-a, total phosphorus, total nitrogen, cyanobacteria, suspended solids, bottom dissolved oxygen, and Secchi depth) to produce reduced sets of orthogonal variables. All data were either log- or fourth-root transformed and subsequently standardised before being used in the analysis. We retained the first and second principal component axes that accounted for 73.8 and 15.2% of the variance in water quality, respectively (Table S1). The positive loading of the first principal component axis (Water PC1) was represented by chlorophyll-a (0.416), total phosphorus (0.411), total nitrogen (0.404), cyanobacteria (0.411), and suspended solids (0.410), while the negative loading was represented by Secchi depth (−0.394). The positive loading of the second principal component axis (Water PC2) was represented by bottom dissolved oxygen (0.945). Water PC1 and Water PC2 were subsequently used as predictors in boosted regression-tree (BRT) models (see below).

When modelling water quality as the response variable, we used the total phosphorus concentration as a major driver of eutrophication and algal blooms in farm ponds. Although some studies have shown evidence of nitrogen limitation in lentic systems (Dolman *et al.*, 2012), the concentrations of total phosphorus and total nitrogen were likewise highly correlated with chlorophyll-a ($r > 0.90$). The importance of landscape variables on farmland biodiversity depends on the spatial scale (Raebel *et al.*, 2012; Usio *et al.*, 2015). Therefore, we used generalised linear models with either Gaussian (identity link) or Poisson distributions (log link) to analyse each of six spatial scales separately in terms of how taxonomic richness of phytoplankton, aquatic plants, zooplankton, macroinvertebrates, fish, and adult odonates responded to the surrounding landscape variables. We selected the best spatial scale on the basis of the lowest Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). We considered only one spatial scale for each biological indicator in further analyses. When none of the spatial scales showed sufficient explanatory power relative to the null model (ΔAIC < 2), we did not include landscape variables as explanatory variables in further analyses.

We used BRT models to investigate the effects of land-use variables (i.e. landscape variables and modern pond management) and fish abundance on the total phosphorus concentration relative to other environmental variables. The BRT approach combines a statistical model (i.e. regression tree model) and machine learning techniques (i.e. boosting), such that boosting is used for adaptively combining large numbers of relatively simple tree models to optimise predictive performance (Elith *et al.*, 2008). We used BRT models because they allow complex or irregular relationships between predictors and responses, which are common in field data (Elith *et al.*, 2008). Prior to the analyses, we checked for collinearity among predictors ($r > 0.70$). Consequently, we removed elevation and the proportion of urban areas, because both variables were highly correlated with the proportions of broadleaved forests, grassland, freshwater, and/or concrete bank construction at many spatial scales. We treated the response variable as having a Gaussian distribution following log transformation. We assessed the relative importance of land-use variables and fish abundance in the following three ways: their frequencies of selection in the BRT model, their partial dependence plots, and their effects on the explained deviance (1 − [residual deviance / null deviance]) expressed as percentages (D^2). We assessed the effects of each land-use variable (at the best spatial scale) and fish abundance on the explained deviance by comparing the explained deviance in the model excluding the land-use variable or fish abundance from predictors to that of the full model. After initial inspections, we implemented

BRT models with a tree complexity of 2 and a bagging fraction of 0.5 with 10-fold cross-validation. A learning rate was set to ensure that at least 1,000 trees were produced during the fitting process (Elith *et al.*, 2008). We performed the BRT modelling in the gbm library (Ridgeway, 2016) in R version 3.3.2 (R Development Core Team, 2016) with an additional R code written by Elith et al. (Elith *et al.*, 2008).

To investigate the influence of changes in the trophic state on taxonomic richness patterns of farm pond communities, we subsequently constructed six BRT models using taxonomic richness of biological indicators as response variables. We defined the clear-water and turbid states as alternative trophic phases along the gradient of Water PC1, where positive loading was represented by eutrophication-related variables, such as chlorophyll-a, total phosphorus, total nitrogen, cyanobacteria, and suspended solids (i.e. turbid state), and negative loading was represented by water transparency (i.e. clear-water state). We assessed the influence of Water PC1 on the taxonomic richness of biological indicators relative to management and other environmental variables. We treated each response variable as having either a Gaussian or Poisson distribution with a tree complexity of 2 and a bagging fraction of 0.5 with 10-fold cross-validation. We assessed the relative importance of water PC1 in three ways using the procedure described above.

In all BRT models, we inspected whether a spatial autocorrelation existed in the residuals of the BRT models using semi-variograms (ncf package; Bjornstad, 2016) and Moran's I statistics (spdep package; Bivand, 2016). When the residual of a BRT model appeared to be spatially autocorrelated (Moran's I: $P < 0.05$), we calculated the residual autocovariate (RAC) (Crase *et al.*, 2012). We applied the inverse distance-weighting scheme to calculate RAC (Dormann *et al.*, 2007).

3. Results

3.1. Farm pond communities

The total number of taxonomic groups identified from the 64 ponds were 336 for phytoplankton, 70 for aquatic plants (excluding 6 non-native species), 132 for zooplankton, 162 for macroinvertebrates (excluding 5 non-native species), 11 for fish (excluding 6 non-native species), and 59 for adult Odonata. The median taxonomic richness of aquatic plants (3.5) and fish (1.0) were relatively low, while those of phytoplankton (39.0), zooplankton (21.0), macroinvertebrates (20.0), and adult Odonata (14.0) were relatively high (Figure 2).

For fish, the native stone moroko (*Pseudorasbora parva* (Cyprinidae)) and the invasive bluegill (*Lepomis macrochirus* (Centrarchidae) dominated the fish assemblages in terms of mean abundance (*Pseudorasbora*: 49.7%; *Lepomis*: 49.1%) and prevalence (*Pseudorasbora*: 37.5%; *Lepomis*: 60.9%).

3.2. Scale-dependent effects of landscape variables on the total phosphorus concentration and taxonomic richness of farm pond communities

The total phosphorus concentration and taxonomic richness of most farm pond communities were at least in part influenced by landscape variables (Table 2). The most relevant spatial scales differed among chemical or biological indicators. Phytoplankton richness (10 and 100 m), zooplankton richness (250 and 500 m), and adult Odonata richness (500 m) were most associated with landscape variables at relatively short-distance spatial scales, while total phosphorus concentration (2,000 m) and macroinvertebrate richness (1,000 and 2,000 m) were most associated with relatively distant spatial scales. Fish richness (10 and 1,000 m) showed associations with multiple spatial scales at short and distant scales. Aquatic plant richness was associated with landscape variables at a 2,000 m scale. However, the AIC value of landscape variables at the 2,000 m scale showed little difference relative to that of the null model (ΔAIC < 2), indicating that the landscape variables were not significant predictors of aquatic plant richness.

3.3. Effects of land use and other environmental variables on total phosphorus concentration

A BRT model for total phosphorus concentration incorporating the best spatial scale of landscape variables (i.e. 2,000 m radius) showed that a high concentration of total phosphorus was associated with shallow water, a low proportion of broadleaved forest areas, a low proportion of grassland areas, a high proportion of paddy field areas, a high proportion of concrete bank construction, high fish abundance, a low proportion of floating-leaved macrophyte coverage, and ponds that use agricultural drainage as the main water source (Figure 3). Among eight predictors that showed significant contributions in explaining total phosphorus concentration, the relative percentage contributions of three surrounding landscape variables and concrete bank construction were moderate to high (8.1–

20.6%), and explained deviance changed from –1.2% to 0.9% when each land-use variable was excluded from the simplified model (Table 3).

Among the four land-use variables, the proportion of broadleaved forest areas had the largest contribution in terms of percentage contribution (20.6%). Fish abundance was also a significant predictor of the total phosphorus concentration of the farm ponds. The percentage contribution of fish abundance (7.1%) was lower than that of the four land-use variables, although the change in explained deviance (1.5%) when the term was excluded from the simplified model was higher than that for any of the land-use variables.

3.4. Effects of clear-water and turbid states on taxonomic richness of farm pond communities

BRT models for taxonomic richness of biological indicators incorporating the best spatial scales of landscape variables showed that high taxonomic richness of aquatic plants, macroinvertebrates, and adult Odonata were associated with a clear-water state while those of phytoplankton and fish were associated with a turbid state (Figure 4, Table 4). For zooplankton, Water PC1 was not retained in the simplified model. For the five taxonomic groups that showed significant associations with trophic states, relative percentage contributions of Water PC1 were moderate (9.0–19.5%), and explained deviance changed from –0.6 to 1.6% when Water PC1 was excluded from the simplified models (Table 4). Therefore, changes in trophic states lead to changes in the taxonomic richness of farm pond communities.

4. Discussion

Our study of 64 farm ponds in western Japan showed that both land use and fish abundance were significant predictors of changes in the trophic state of ponds and that such changes are reflected in the taxonomic richness patterns of farm pond communities. In subsequent sections, we discuss the landscape responses of total phosphorus and the taxonomic richness of farm pond communities, effects of land use and fish abundance on the total phosphorus concentration of farm ponds, effects of changes in the trophic state on the patterns of taxonomic richness of farm pond communities, and management strategies for farm ponds with regard to trophic states and biodiversity.

4.1 Landscape responses of total phosphorus and taxonomic richness of farm pond communities

The total phosphorus concentration, a main driver of changes in the trophic state, and the taxonomic richness of six biological indicators were associated with landscape variables from no distance (aquatic plants) to relatively short distance (phytoplankton: 10 and 100 m; zooplankton: 250 and 500 m; adult Odonata: 500 m), through to long-distance scales (total phosphorus: 2,000 m; macroinvertebrates: 1,000 and 2,000 m). In contrast, the taxonomic richness of fish was associated with both short- and distant-spatial scales (10 and 1,000 m). Researchers have indicated that the occurrence of specific species is generally associated with landscape factors depending on their ecological characteristics, such as life stages or growth forms (Akasaka *et al.*, 2010; Raebel *et al.*, 2012; Usio *et al.*, 2014). For example, Raebel *et al*. (2012) showed that dragonflies were associated with landscape factors at long-distance scales, while damselflies were associated with short-distance scales. A possible reason that fish richness was associated with both short- and long-distance scales is that the occurrences of certain species were associated with different spatial scales depending on their dispersal abilities.

4.2 Relative effects of land use and fish abundance on the total phosphorus concentration of farm ponds

The total phosphorus concentration was significantly associated with low coverage of broadleaved forest and grassland at a 2,000-m radius, high coverage of paddy fields at a 2,000-m radius, and a high proportion of concrete bank construction. Furthermore, the total phosphorus concentration of farm ponds was also associated with shallow water depth, high fish abundance, low coverage of floating-leaved macrophytes, and farm ponds that used agricultural drainage as the main water source. Thus, land use, fish abundance, and other environmental variables were all important in determining the trophic states of farm ponds. As evident from the change in percentage deviance after excluding the variable from the simplified model, fish abundance had as influential an effect on trophic states as did the land-use variables.

We suspect that feeding activities by the stone moroko and bluegill, which dominate farm pond fish assemblages, had significant effects on the trophic state of farm ponds. Japanese cyprinid fishes are generally omnivores that feed on macroinvertebrates, periphyton, sediments, and zooplankton (Kawanabe *et al.*, 1989). Bluegill are also omnivores that feed on macrophytes, zooplankton, and macroinvertebrates (Uchii *et al.*, 2007). Bioturbation activities of fish through benthic feeding may enhance the nutrient concentration via sediment resuspension and excretion (Matsuzaki *et al.*, 2007).

In contrast, surrounding vegetation coverage seemed to act as a buffer for eutrophication and sedimentation by suppressing surface run-off through evapotranspiration and filtering the nutrients in the water (Bosch and Hewlett, 1982). In addition, when correlation analyses were performed among landscape variables at a 2,000-m radius, the coverage of broadleaved forest showed a strong, negative correlation with the coverage of urban areas ($r = -0.78$). Likewise, the coverage of grassland at a 2,000-m radius showed a moderately high correlation with the coverage of urban areas ($r = -0.66$). Therefore, low coverages of broadleaved forest and grassland are indicators of urbanisation. Urban areas and paddy fields function as sources for non-point pollution (Carpenter *et al.*, 1998). Surface run-off containing rich nutrients from urban and agricultural areas may result in loss of macrophytes, which in turn leads to a turbid state.

Macrophytes play key roles in maintaining a clear water state in shallow lentic systems through various ecological functions, including absorbing nutrients from the water column, suppressing sediment resuspension, releasing nitrogen in the atmosphere through denitrification, releasing allelochemicals, and providing refuge habitats for zooplankton grazers and thereby indirectly suppressing phytoplankton through a trophic cascade (Jeppesen, 1998). However, farm ponds with a high proportion of concrete bank construction may result in the loss of shallow coastal areas (ecotones), crucial habitats for macrophytes because of the high light availability. Likewise, Casas *et al.*, (2011) reported that concrete ponds have high slope angles at their margins and are therefore associated with depauperate marginal vegetation although we have no direct evidence to test this hypothesis. We found a negative relationship between aquatic plant richness and concrete bank construction (Figure S1) and a positive relationship between the total phosphorus concentration and concrete bank construction (Figure 3). Furthermore, farm ponds with high phosphorus concentration were also associated with extremely low coverage of floating-leaved macrophytes (Figure 3). Therefore, concrete bank construction had a positive association with a high total phosphorus concentration, at least in part through loss of macrophytes and their associated ecological functions.

4.3 Effects of changes in the trophic state on the taxonomic richness patterns of farm pond communities

A clear-water state was associated with high taxonomic richness of aquatic plants, macroinvertebrates, and adult Odonata, while a turbid state was associated with high taxonomic richness of phytoplankton and fish. Among the biological indicators that showed associations with trophic states, clear-water or turbid states had the greatest impact on the taxonomic richness of macroinvertebrates and phytoplankton, as indicated by the percentage change in deviance after Water PC1 was excluded from the respective simplified models. Although live macrophytes contain chemical compounds that deter direct grazing of aquatic animals, herbivorous–detritivorous macroinvertebrates can utilise decayed plant tissue, trapped sediments, and periphyton in macrophytes as food sources. Furthermore, the structural complexity of macrophytes is important in terms of providing refuge sites for macroinvertebrates, including predatory taxa (Taniguchi *et al.*, 2003; Kovalenko *et al.*, 2012). In addition, many dragonflies and damselflies rely on macrophytes as spawning, resting, and hatching sites (Corbet, 1999; Butler and deMaynadier, 2008). Therefore, macrophytes play important roles as indicators of a clear-water state, as well as autogenic ecosystem engineers.

4.4 Implications for farm pond management

Our results have important implications for conservation and restoration of farm ponds. First, coverage of broadleaved forest and grassland were among the significant variables that affected the trophic states of farm ponds. In terms of designating conservation areas, farm ponds surrounded by rich broadleaved forest and grassland at a 2,000-m radius from the ponds may be set as high-priority conservation areas because such ponds likely show a clear-water state represented by the presence of diverse aquatic plants, adult Odonata, and macroinvertebrates. The information on surrounding land use may also be used when creating a new pond; pond creation with the aim of restoring degraded biodiversity in the area may be successful in a location surrounded by grassland and/or broadleaved forest. However, caution is needed when selecting pond conservation or restoration sites in relation to vegetation structure because the influence of landscape factors is scale dependent, as shown in this and past studies (Akasaka *et al.*, 2010; Raebel *et al.*, 2012).

In Europe, conservation of a clear-water state and high vegetation complexity in both existing and newly created farm ponds has been suggested as important in landscapes dominated by cropland, provided that the farmland is extensively managed (Declerck *et al.*, 2006). However, this may not apply in paddy-dominated landscapes in Japan, in which each paddy field is generally small (< 1 ha), extensively managed paddy fields are sporadically distributed, and paddy fields are generally intensively managed at the regional level. Recently, increased attention has been paid to environmentally friendly farming (Usio, 2014). The main reason to implement environmentally friendly farming is to develop multiple functions of farmland beyond their role of producing food (i.e. multi-functionality of agriculture). For this purpose, various environmentally farming practices have been implemented, including wildlife-friendly farming (Usio, 2014). Halving or omitting the use of agrochemicals is the base procedure for all environmentally friendly farming practices. Conservation or restoration of farm ponds within paddy-dominated landscapes may become successful if the arrangement and size of environmentally friendly paddy fields are appropriately considered. For example, environmentally friendly farming may be implemented in a block rather than individually along the area connected by a single agricultural drainage system. In this way, the release of nutrient-rich effluent from paddy fields to agricultural drainage may be mitigated more efficiently.

Pond management also plays a key role in determining the trophic states of farm ponds, because management practices affect the water quality of such ponds (Bonachela *et al.*, 2013). In the past few decades, management styles of farm ponds have changed to minimise labour. In recent decades, concrete bank construction has been commonly employed to facilitate pond maintenance by avoiding erosion of banks. Whenever possible, concrete bank construction should be avoided to maintain farm ponds in a clear-water state. When it is unavoidable, care should be taken to maintain or create ecotones to facilitate macrophyte growth. In contrast, pond draining was commonly performed after rice harvest to catch fish as a social event until about the 1960s. Such fish catches were not only important as social events to facilitate mingling with other residents in the village but probably also important as “biomanipulation” through the removal of cyprinid fish. In recent decades, pond draining is no longer practised in most locations in the study region, due to aging and depopulated regional communities (Takamura, 2012). Even if pond draining has taken place, the practice is often not followed by a fish catch. A previous study reported that pond draining per se had little effect on the water quality of farm ponds (Usio *et al.*, 2013). However, revitalisation of pond draining combined with fish catches may have the potential to maintain a clear-water state of farm ponds, provided that fish immigration from water sources is managed appropriately. Nevertheless, caution is needed when performing fish catches in a region invaded by the red swamp crayfish, as pond draining followed by fish-catches (or fish eradication) may facilitate invasion by this non-native crayfish species (Usio *et al.*, 2009; Usio *et al.*, 2013). In such regions, the crayfish should be concurrently managed, possibly through mechanical crayfish removal together with the conservation of carnivorous fish predators (e.g. Japanese eel *Anguilla japonica*, Japanese common catfish *Silurus asotus*) and their habitats.

Limitations of our study include its scope and analyses. In Japan, pond managers are generally concerned about the water quality of farm ponds, because pond water is used primarily for irrigated farming. Specifically, more than 54% of all farmland area in Japan comprises rice paddy fields (e-Stat, 2017). In rice farming, water quality, together with soil type and diurnal temperature variation, is of primary importance in determining rice grain quality and yield (Hirai *et al.*, 2010). Given that a major focus of farm pond management in Japan is to maintain good water quality, biodiversity patterns in Japanese farm ponds are presumably determined primarily by water quality. Nevertheless, we incorporated water-quality and water management variables to a limited degree in the analyses. Furthermore, the primary focus of agro-ecosystem management is to enhance or secure crop productivity. Therefore, crop productivity may also be a significant determinant of biodiversity patterns in farm ponds. In regions where agricultural drainage is used as a main water source for farm ponds and/or where upper areas are intensively managed as farmland, crop productivity may also influence water quality due to the amount of fertilisers used on farmland. Future studies should encompass productivity indicators together with various water-quality indicators, farming practices, and water management toward a comprehensive understanding of the biodiversity patterns in farm ponds.

5. Conclusions

In summary, our findings show that land-use effects and fish abundance are major stressors leading to changes in trophic state and that the taxonomic richness of phytoplankton, aquatic plants, macroinvertebrates, fish, and adult Odonata change along the gradient of trophic states, but with the differential strength of such effects being relative to other local and landscape factors (Figure 5). Identifying the ecological thresholds of changes in the trophic states and multi-taxonomic diversity responses may be crucial for the design of plans for restoration of degraded farm ponds.

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Table 1. Summary statistics of 64 farm ponds in western Japan.

Variables	Mean	SD	Range or category
Biotic variables			
phytoplankton (no. taxa)	39.5	14.9	5–72
aquatic plant (no. taxa)	5.5	5.3	0–22
zooplankton (no. taxa)	20.6	5.2	9–34
macroinvertebrate (no. taxa)	19.6	7.7	6–48
fish (no. taxa)	1.5	1.3	0–4
adult Odonata (no. taxa)	14.9	6.2	4–30
bluegill occurrence	NA	NA	presence, absence
red swamp crayfish occurrence	NA	NA	presence, absence
fish abundance (catch per unit effort)	93.1	134.2	0–523
floating-leaved macrophyte coverage (%)	17.9	30.1	0–94.1
Water-quality variables			
cyanobacteria (cell mL^{-1})	11,932	21,180	0–74,379
bottom dissolved oxygen (mg L^{-1})	3.6	3.3	0.3–11.3
chlorophyll-a (μg L^{-1})	72.4	102.9	1–438
total phosphorus (mg L^{-1})	0.13	0.14	0.01–0.68
total nitrogen (mg L^{-1})	1.32	1.30	0.20–5.61
suspended solids (mg L^{-1})	20.7	21.6	1.5–127.8
Secchi depth (m)	0.7	0.6	0.1–3.6
Morphometric variables			
pond surface area (ha)	1.10	1.48	0.08–11.43
water depth (m)	1.7	1.1	0.1–4.8
Geographical variable			
elevation (m)	58.2	33.6	8.0–133.7
Landscape variables			
freshwater (%)	3.8	3.6	0–18.7
broadleaved forest (%)	25.9	29.4	0–91.9
paddy field (%)	32.1	21.2	0–80.6
cropland (%)	3.6	5.8	0–23.5
grassland (%)	15.0	13.1	0–70.6
urban area (%)	19.6	23.2	0–93.0
Pond management			
concrete bank construction (%)	44.5	36.4	0–100.0
pond draining	NA	NA	undrained, partially-drained, drained
water source	NA	NA	agricultural drain, dam, natural

Table 2. Scale-dependent effects of landscape variables on the total phosphorus concentration and taxonomic richness of farm pond communities on the basis of generalised linear models. The smallest Akaike's information criterion (AIC) value in each model is indicated in bold typeface.

	Concentration	Taxonomic richness					
Spatial scale	Total phosphorus	Phyto-plankton	Aquatic plant	Zoo-plankton	Macro-invertebrate	Fish	Adult Odonata
Null	196.29	530.13	**152.79**	396.84	63.21	207.71	-15.54
10	167.76	**514.33**	157.53	401.27	60.88	**197.38**	-24.28
100	164.02	514.92	158.39	397.99	57.79	203.28	-30.38
250	166.22	519.61	157.46	**393.68**	58.28	204.13	-36.35
500	163.33	522.74	156.72	395.16	56.34	203.36	**-38.89**
1000	170.05	532.09	156.35	398.70	54.81	198.87	-31.14
2000	**158.70**	529.29	153.77	398.46	**53.85**	202.72	-34.28

Table 3. Contributions of land-use (i.e. landscape variables and modern pond management), fish abundance, and other environmental variables to the total phosphorus concentration in boosted regression-tree models. The contribution of each variable was assessed by the percentage deviance (D^2) explained after exclusion of each variable from the simplified model. Small letters in brackets (a to f) refer to the labels. Percentage contributions of each land-use variable and fish abundance were calculated based on the formula shown in the brackets.

Source	Total phosphorus concentration (mg L^{-1})
Water PC1	–
Water PC2	–
Floating-leaved macrophyte coverage	6.2
Aquatic plant richness	removed
Fish abundance	7.1
Bluegill occurrence	removed
Red swamp crayfish occurrence	removed
Pond surface area	removed
Water depth	23.4
Pond draining	removed
Water source	5.6
Concrete bank construction	8.1
FRW2000	removed
BRF2000	20.6
PDF2000	11.6
CRO2000	removed
GRA2000	17.4
Percentage deviance explained	
simplified model (a)	59.9
without GRA2000 (b)	61.0
without BRF2000 (c)	58.9
without PDF2000 (d)	59.6
without concrete bank construction (e)	60.5
without fish abundance (f)	58.3
% contribution of GRA2000 (a−b)	-1.2
% contribution of BRF2000 (a−c)	0.9
% contribution of PDF2000 (a−d)	0.3
% contribution of concrete bank construction (a−e)	-0.7
% contribution of fish abundance (a−f)	1.5

The notation "–" indicates that the variable was not used as a predictor in the model. See text and Table S1 for significant principal component loadings of water-quality variables (Water PC1-2). The number in the landscape variables indicates the buffer radius used to calculate the coverage of the surrounding landscape component. FRW = freshwater, BRF = broadleaved forest, PDF = paddy field, CRO = cropland, GRA = grassland.

Table 4. Percentage contributions of predictors and model performance with and without Water PC1 in simplified, boosted regression-tree models.

Source	Taxonomic richness					
	Phytoplankton	Aquatic plant	Zooplankton	Macroinvertebrate	Fish	Adult Odonata
Water PC1	18.5	10.1	removed	19.5	14.6	9.0
Water PC2	removed	13.7	removed	10.3	removed	removed
Floating-leaved macrophyte coverage	10.2	34.9	14.8	removed	removed	4.2
Aquatic plant richness	removed	–	removed	20.6	removed	16.9
Fish abundance	13.6	removed	removed	removed	31.5	7.7
Bluegill occurrence	removed	removed	15.6	removed	removed	2.7
Red swamp crayfish occurrence	removed	removed	removed	removed	removed	removed
Pond surface area	14.5	10.6	20.2	removed	removed	6.6
Water depth	removed	11.1	removed	removed	10.6	9.7
Pond draining	removed	removed	removed	removed	removed	removed
Water source	removed	6.5	removed	removed	removed	removed
Concrete bank construction	10.4	13.2	removed	28.6	removed	11.3
FRW10	removed	–	–	–	removed	–
BRF10	26.0	–	–	–	24.4	–
PDF10	6.8	–	–	–	removed	–
CRO10	removed	–	–	–	removed	–
GRA10	removed	–	–	–	removed	–
FRW250	–	–	18.6	–	–	–
BRF250	–	–	removed	–	–	–
PDF250	–	–	30.9	–	–	–
CRO250	–	–	removed	–	–	–
GRA250	–	–	removed	–	–	–
FRW500	–	–	–	–	–	removed

Table 4 (continued)

Source	Taxonomic richness					
	Phytoplankton	Aquatic plant	Zooplankton	Macroinvertebrate	Fish	Adult Odonata
BRF500	–	–	–	–	–	20.8
PDF500	–	–	–	–	–	11.2
CRO500	–	–	–	–	–	removed
GRA500	–	–	–	–	–	removed
FRW1000	–	–	–	–	–	–
BRF1000	–	–	–	–	–	–
PDF1000	–	–	–	–	–	–
CRO1000	–	–	–	–	–	–
GRA1000	–	–	–	–	–	–
FRW2000	–	–	–	removed	–	–
BRF2000	–	–	–	10.2	–	–
PDF2000	–	–	–	removed	–	–
CRO2000	–	–	–	removed	–	–
GRA2000	–	–	–	10.7	–	–
RAC	–	–	–	–	18.9	–
Deviance explained (%)						
simplified model	19.3	33.4	17.3	20.9	21.1	48.8
with water PC1	19.3	33.4	15.4	20.9	21.1	48.8
without water PC1	17.7	33.2	17.3	20.3	21.7	48.8
% contribution of water PC1	1.6	0.2	–	0.7	-0.6	0

The notation "–" indicates that the variable was not used as a predictor in the model. The notation "removed" indicates that the variable was removed from the simplified model. See text and Table S1 for significant principal component loadings of water-quality variables (Water PC1-2). FRW = freshwater, BRF = broadleaved forest, PDF = paddy field, CRO = cropland, GRA = grassland, RAC = residual autocovariate.

Figure legends

Figure 1. Map of the 64 farm ponds in Hyogo Prefecture, Japan.

Figure 2. Taxonomic richness of six biological indicators of 64 farm ponds in western Japan. The main taxonomic resolutions are species for aquatic plants, phytoplankton, zooplankton, fish, and adult Odonata, and genus for macroinvertebrates. The thick lines show the medians, and the boxes delineate the interquartile ranges. The whiskers denote 1.5 times the interquartile range. Small circles above the whiskers indicate outliers.

Figure 3. Partial plots of the effects of land-use variables (landscape variables and modern pond management), fish abundance, and other environmental variables on the total phosphorus concentration in the simplified, boosted regression-tree model. The fitted function represents the effects of the selected variable on the response variable. Relative contributions of predictor variables are shown in parentheses. Rug plots inside the top of each plot show the distribution of sites across the variable in deciles. The number in the landscape variables indicates the buffer radius used to calculate the coverage of the surrounding landscape component. BRF = broadleaved forests, GRA = grassland, PAD = paddy field, CPUE = catch per unit effort.

Figure 4. Partial plots of the effects of Water PC1 (the first principal component axis from a principal component analysis (PCA) of seven water-quality variables; see text) on taxonomic richness of five biological indicators in the simplified, boosted regression-tree models. The fitted function represents the effects of the selected variable on the response variable. The relative contributions of predictor variables are shown in parentheses. Rug plots inside the top of each plot show the distribution of sites across the variable in deciles.

Figure 5. Conceptual model summarising the results of the study. Thick arrows indicate strong effects (not to scale).

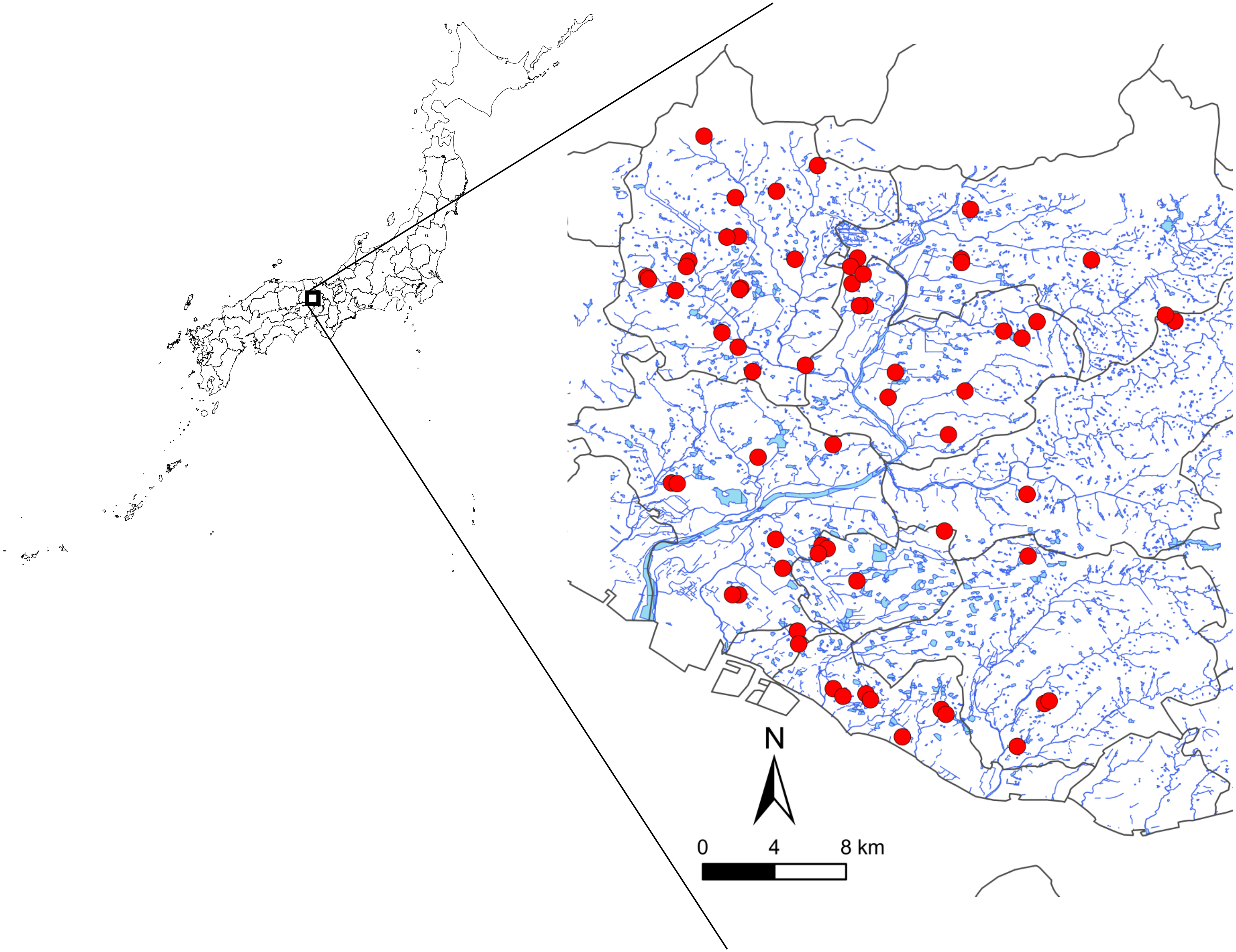

Fig. 1 Usio et al.

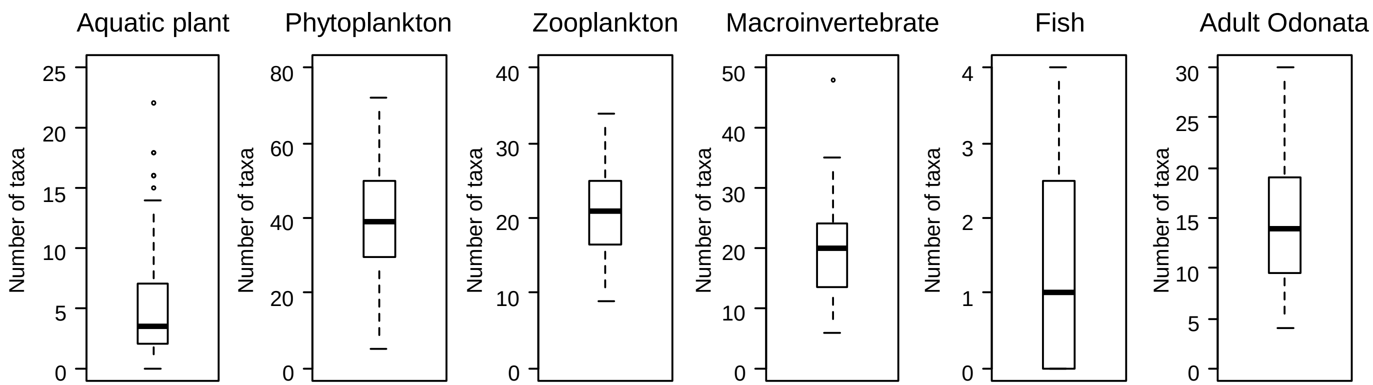

Fig. 2 Usio et al.

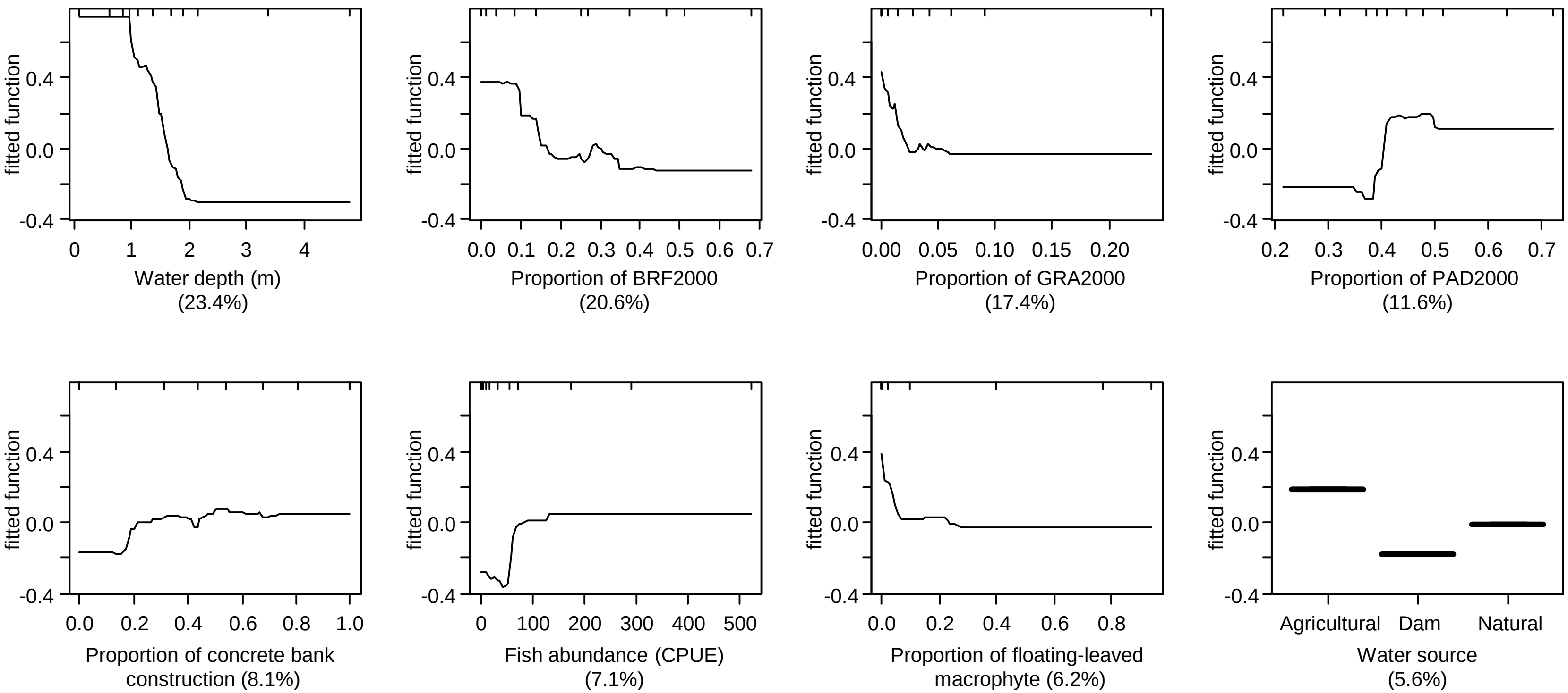

Fig. 3 Usio et al.

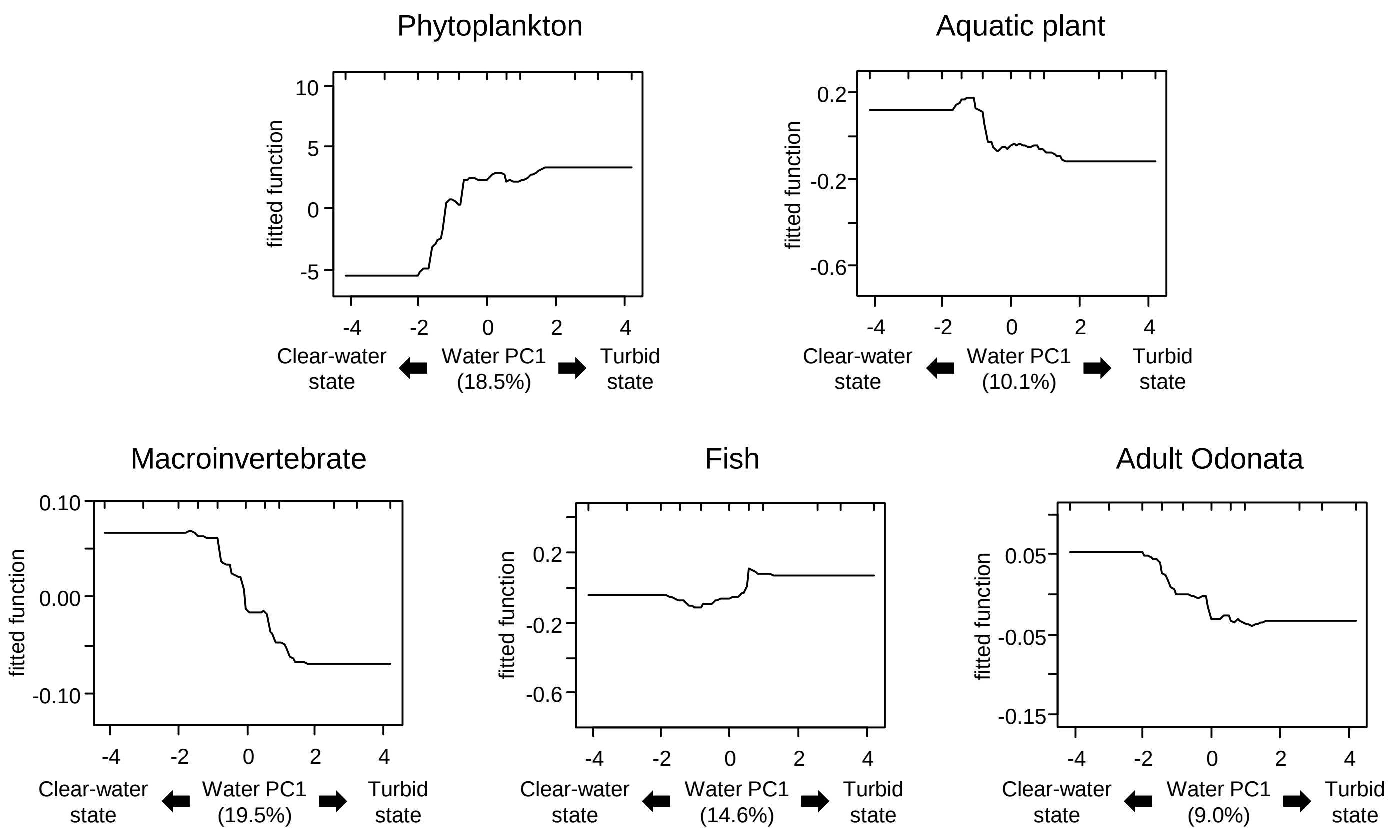

Fig. 4 Usio et al.

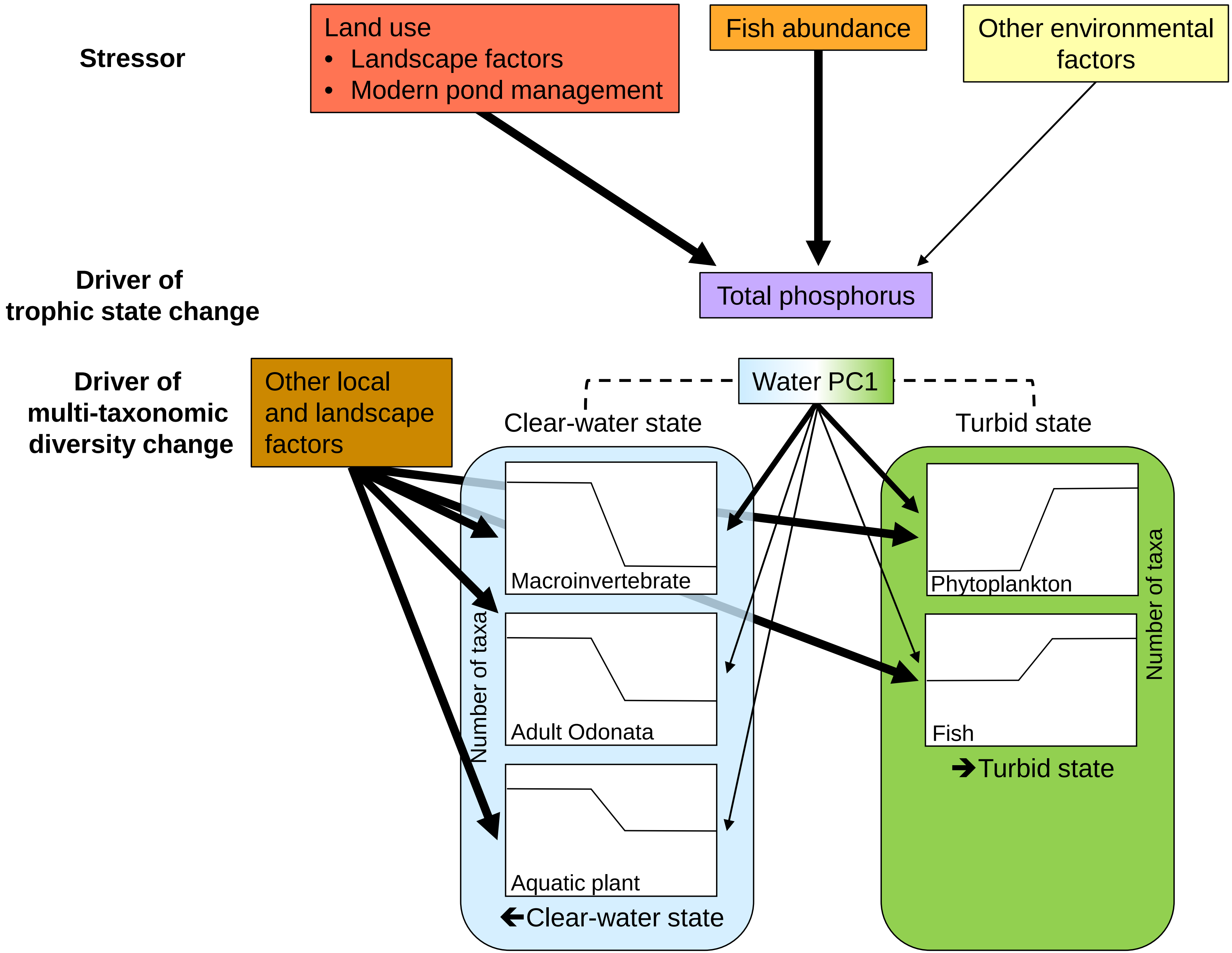

Fig. 5 Usio et al.

Supplementary materials

Table S1. Loadings of the first two principal component axes for water-quality variables in the principal component analysis (PCA).

Water quality	Water PC1	Water PC2
chlorophyll-a (μg L^{-1})	0.416	-0.165
total phosphorus (mg L^{-1})	0.411	-0.106
total nitrogen (mg L^{-1})	0.404	-0.129
cyanobacteria (cells mL^{-1})	0.411	-0.020
suspended solids (mg L^{-1})	0.410	0.128
bottom dissolved oxygen (mg L^{-1})	0.049	0.945
Secchi depth (m)	-0.394	-0.186
eigenvalue	5.164	1.065
proportion of variance explained	0.738	0.152
cumulative proportion	0.738	0.890

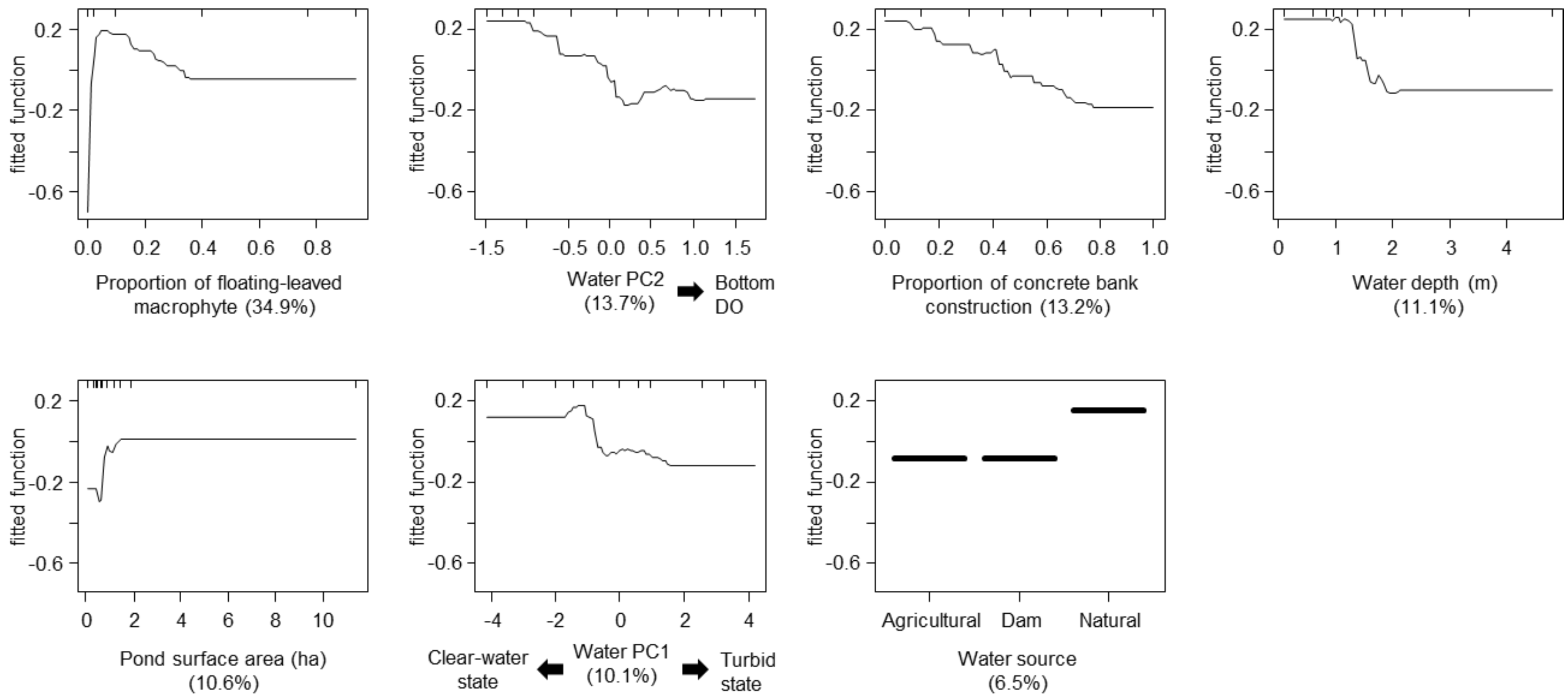

Figure S1. Partial plots of the effects of land-use (concrete bank construction) and other environmental variables on the taxonomic richness of aquatic plants in the simplified, boosted regression-tree model. The fitted function represents the effects of the selected variable on the response variable. Relative contributions of predictor variables are shown in parentheses. Rug plots inside the top of each plot show the distribution of sites across the variable in deciles. Water PC1 and Water PC2 refer to the first and second principal component axes from a principal component analysis (PCA) of seven water quality variables (see text and Table S1). Bottom DO = bottom dissolved oxygen.