

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

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

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4 Nisikawa Usio ^{a,*} Megumi Nakagawa ^b, Takashi Aoki ^c, Shinsuke Higuchi ^d, Yasuro Kadono ^d,

5 Munemitsu Akasaka ^e and Noriko Takamura ^b

6 ^a *Institute of Nature and Environmental Technology, Kanazawa University, Kanazawa 920-1192,*
7 *Japan*

8 ^b *Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental*
9 *Studies, Tsukuba 305-8506, Japan*

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

12 ^d *Graduate School of Science, Kobe University, Kobe 657-8501, Japan*

13 ^e *Tokyo University of Agriculture and Technology, Tokyo 183-8509, Japan*

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

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

17

18 **Abstract**

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

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

35 **1. Introduction**

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

47 Despite the common view that anthropogenic ecosystems have low levels of biodiversity, recent
48 studies have shown that water bodies in agricultural and urban landscapes, such as farm ponds,
49 highway ponds, paddy fields, and irrigation ditches, play important roles in biodiversity conservation
50 (Elphick, 2000; Cereghino *et al.*, 2008; Le Viol *et al.*, 2009; Negishi *et al.*, 2014; Wezel *et al.*, 2014).
51 Farm ponds in particular have been shown to be among the most biodiverse water bodies because of
52 their small size, shallow water depth, and aquatic vegetation (Williams *et al.*, 2004; Davies *et al.*,
53 2008). Developing strategies to manage the multiple functions of anthropogenic freshwater ecosystems
54 beyond their roles of irrigating, cropping, or controlling storm water is a key challenge in conservation
55 science.

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

63 Farm ponds have alternative stable states characterised by different trophic states: a clear-water
64 state and a turbid state (Declerck *et al.*, 2006; Phillips *et al.*, 2016). Previous studies have reported that
65 changes from a clear-water state to a turbid state in shallow lakes or ponds are caused by various
66 abiotic and biotic stresses. For example, non-point source pollution from farmland and urban areas is a
67 major factor that enhances nutrient input into shallow lentic systems (Carpenter *et al.*, 1998). Land-use
68 changes, such as deforestation in the surrounding area and input of agrochemicals through agricultural
69 intensification, have been reported to deteriorate water quality and reduce the species richness of
70 aquatic plants in farm ponds (Akasaka *et al.*, 2010). Ecosystem engineering via bioturbation activities
71 by fish or macrophyte cutting and destruction by non-native crayfish are among the major factors that
72 cause macrophyte reduction (Rodriguez *et al.*, 2005; Matsuzaki *et al.*, 2007; Scheffer and van Nes,
73 2007). Furthermore, fish predation on zooplankton can have positive effects on phytoplankton via
74 trophic cascades (Vanni *et al.*, 1997). In most cases, such abiotic and biotic stresses are associated with
75 trophic state changes via increased concentration of phosphorus and/or nitrogen (Jeppesen *et al.*, 1997;
76 Declerck *et al.*, 2006)

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

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

99 **2. Methods**

100 *2.1. Study site*

101 We used a database of biota (phytoplankton, aquatic plants, zooplankton, benthic
102 macroinvertebrates, adult odonates, invasive animals, and floating-leaved macrophyte coverage), water
103 quality, morphometric variables, landscape variables, and pond management at 64 farm ponds in the
104 Kako River Basin of Hyogo Prefecture in western Japan (Takamura, 2011) (Figure 1, Table 1). Land-

105 use variables consisted of both landscape variables (coverage of broadleaved forests, paddy fields,
106 cropland, grassland, urban area, and freshwater within six multi-scale buffers ranging from 10 m to
107 2,000 m in radius) and modern pond management (coverage of concrete bank protection) (see below).
108 Although the detailed history of each farm pond is unknown, most farm ponds in this region were
109 created in the 19th century for the purposes of providing irrigation water to rice paddy fields.

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

119 2.2. Pond surveys

120 From April through November of 2006 and 2008, we sampled the farm ponds to assess water
121 quality and taxonomic richness of phytoplankton, aquatic plants, zooplankton, macroinvertebrates,
122 fish, and adult odonates. We used the six taxonomic groups as biological indicators because these
123 groups are major components of farm pond communities and/or are generally taxon rich, and they are
124 therefore suitable for bio-assessment based on taxonomic richness patterns. For phytoplankton,
125 zooplankton, and water-quality samples, we performed a rapid assessment (without subsamples) at the
126 64 ponds over a relatively short period (7 days) in a single year to minimise temporal variation. For
127 other biological indicators, we performed surveys over 2 or 3 years for logistical reasons. We also
128 surveyed the occurrence (presence or absence) of two widely-distributed invasive species that can
129 affect the water quality and taxonomic richness of biological indicators (see below). We performed a
130 water-quality survey when nutrient concentrations would likely be highest (i.e. warmest month). For
131 biological variables, we made sure to include the seasons when each taxonomic group would likely be
132 at its highest abundance based on past experience with farm pond systems.

133 2.2.1. Water quality

134 From 23 to 29 August 2007, when cyanobacteria blooms were observed in some eutrophic farm
135 ponds, we measured the water transparency (Secchi depth) and concentrations of chlorophyll-a, total
136 phosphorus, total nitrogen, cyanobacteria, suspended solids, and bottom dissolved oxygen of each
137 pond. At each farm pond, we took one measurement or sample for each water quality variable. We
138 measured the concentration of cyanobacteria 20 cm below the water surface using a multiparameter
139 water-quality sonde (YSI6600; YSI, Yellow Spring, Ohio) and dissolved oxygen immediately above
140 the pond bottom using a dissolved oxygen meter (YSI58; YSI). By analysing a 2 L sample of surface
141 water collected from each pond, we determined in the laboratory the concentration of total phosphorus
142 by the ascorbic acid method (APHA, 1998), total nitrogen by the persulfate digestion method (APHA,
143 1998), suspended solids by drying (103°C for 1 h) and combusting (550°C for 1 h) duplicate filtered
144 subsamples, and chlorophyll-a using a spectrophotometric method after extraction in 99% methanol
145 (Marker *et al.*, 1980).

146 2.2.2. Phytoplankton

147 From 23 to 29 August 2007, we collected a water sample from 20 cm below the water surface of the
148 deepest part of each pond using a 100-mL plastic bottle. At each farm pond, we took one water-
149 phytoplankton sample. Following collection of each sample, we added several drops of Lugol's
150 solution for sample preservation. In the laboratory, we used the sedimentation procedure (Utermöhl,
151 1958) to identify phytoplankton (mostly to the species level except for unidentifiable taxa) with the aid
152 of an inverted microscope (400×). At each farm pond, we calculated total number of taxa as a measure
153 of the taxonomic richness of phytoplankton.

154 2.2.3. Aquatic plants

155 From August to September 2006 and 2007, we recorded the occurrence of free-floating
156 macrophytes, floating-leaved macrophytes, emergent macrophytes, and submerged macrophytes
157 including charophytes in the study ponds while walking along the perimeter of the ponds. For deeper
158 parts, we took a floater or boat out onto ponds and raked or lobbed a grapnel (a rake-like device
159 mounted on a rope) on the pond bottom. Aquatic plants were identified mainly to the species level. At

160 each farm pond, we calculated the total taxonomic richness of aquatic plants based on the one-time
161 summer survey.

162 2.2.4. Zooplankton

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

172 2.2.5. Macroinvertebrates

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

182 2.2.6. Fish and invasive species

183 From August to September 2006 and 2007, we sampled fish and decapod crustaceans by setting two
184 fixed fishing nets (width 600 cm, length 304 cm, openings 69 cm, mesh size 4 cm) overnight along the
185 perimeter of each pond and five baited (dried squid and fish sausages) box-shaped minnow traps (25 \times
186 25 cm, length 40 cm, openings 6 cm, mesh size 2 mm) overnight at points equally spaced along the

187 long axis of each pond. The following morning, we identified the animals in the nets and traps. We
188 captured fish, decapod crustaceans, amphibians, and reptiles. In the present paper, however, we
189 consider the data only for fish and the red swamp crayfish (*Procambarus clarkii*). We did not include
190 amphibians in the analyses because no indigenous amphibian species were captured, probably because
191 the survey was not performed when most indigenous amphibians spawn (early spring). We also
192 excluded reptiles (turtles) from the analyses because the only indigenous turtle species (*Mauremys*
193 *japonica*) was rare (occurred in only 4 of 64 sites) in the study ponds. At each farm pond, we
194 calculated the total taxonomic richness and abundance (catch per unit effort) of fish using combined
195 data from the fixed-net fishing and trapping.

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

200 2.2.7. Adult odonates

201 At each pond, we surveyed adult odonates between April and November (with the exception of
202 August) of 2006 and 2008, for a total of six times. On average, we surveyed each pond for 22 min (\pm
203 14 SD) while walking the accessible parts of the pond perimeter or paddling along the pond margin.
204 To avoid misidentification, we recorded sighted adult odonates using a video camera (DCR-HC96,
205 SONY Inc., Japan). We identified most adult dragonflies to the species level by sight and later
206 confirmed using the video recordings. For damselflies and Gomphidae, we identified individuals from
207 samples collected using a sweep net or from the video recordings. In the subsequent statistical model,
208 we used the total number of adult odonate species found at each farm pond during the six surveys.

209 2.3. Landscape variables

210 For each farm pond, we used ArcGIS version 9.1 (ESRI, Redlands, California) to calculate the
211 coverage (proportions) of broadleaved forests, paddy fields, cropland, grassland, urban area, and
212 freshwater within six multi-scale buffers ranging from 10 m to 2,000 m in radius (i.e. 10, 100, 250,
213 500, 1000, 2000 m). We created buffers from the edge of each farm pond that had a shape identical to
214 that of the pond. Within these buffers, we calculated the coverage of each landscape factor using a

215 land-use map (scale: 1:25,000) of the Japan Integrated Biodiversity Information System (Ministry of
216 the Environment, 2000).

217 *2.4. Pond management*

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

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

230 *2.5. Data analysis*

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

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

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

273 BRT models with a tree complexity of 2 and a bagging fraction of 0.5 with 10-fold cross-validation. A
274 learning rate was set to ensure that at least 1,000 trees were produced during the fitting process (Elith
275 *et al.*, 2008). We performed the BRT modelling in the gbm library (Ridgeway, 2016) in R version
276 3.3.2 (R Development Core Team, 2016) with an additional R code written by Elith *et al.* (Elith *et al.*,
277 2008).

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

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

294 **3. Results**

295 *3.1. Farm pond communities*

296 The total number of taxonomic groups identified from the 64 ponds were 336 for phytoplankton, 70
297 for aquatic plants (excluding 6 non-native species), 132 for zooplankton, 162 for macroinvertebrates
298 (excluding 5 non-native species), 11 for fish (excluding 6 non-native species), and 59 for adult
299 Odonata. The median taxonomic richness of aquatic plants (3.5) and fish (1.0) were relatively low,

300 while those of phytoplankton (39.0), zooplankton (21.0), macroinvertebrates (20.0), and adult Odonata
301 (14.0) were relatively high (Figure 2).

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

305 3.2. Scale-dependent effects of landscape variables on the total phosphorus concentration and 306 taxonomic richness of farm pond communities

307 The total phosphorus concentration and taxonomic richness of most farm pond communities were at
308 least in part influenced by landscape variables (Table 2). The most relevant spatial scales differed
309 among chemical or biological indicators. Phytoplankton richness (10 and 100 m), zooplankton richness
310 (250 and 500 m), and adult Odonata richness (500 m) were most associated with landscape variables at
311 relatively short-distance spatial scales, while total phosphorus concentration (2,000 m) and
312 macroinvertebrate richness (1,000 and 2,000 m) were most associated with relatively distant spatial
313 scales. Fish richness (10 and 1,000 m) showed associations with multiple spatial scales at short and
314 distant scales. Aquatic plant richness was associated with landscape variables at a 2,000 m scale.
315 However, the AIC value of landscape variables at the 2,000 m scale showed little difference relative to
316 that of the null model ($\Delta AIC < 2$), indicating that the landscape variables were not significant
317 predictors of aquatic plant richness.

318 3.3. Effects of land use and other environmental variables on total phosphorus concentration

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

327 20.6%), and explained deviance changed from -1.2% to 0.9% when each land-use variable was
328 excluded from the simplified model (Table 3).

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

335 *3.4. Effects of clear-water and turbid states on taxonomic richness of farm pond communities*

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

345 **4. Discussion**

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

353 *4.1 Landscape responses of total phosphorus and taxonomic richness of farm pond communities*

354 The total phosphorus concentration, a main driver of changes in the trophic state, and the taxonomic
355 richness of six biological indicators were associated with landscape variables from no distance (aquatic
356 plants) to relatively short distance (phytoplankton: 10 and 100 m; zooplankton: 250 and 500 m; adult
357 Odonata: 500 m), through to long-distance scales (total phosphorus: 2,000 m; macroinvertebrates:
358 1,000 and 2,000 m). In contrast, the taxonomic richness of fish was associated with both short- and
359 distant-spatial scales (10 and 1,000 m). Researchers have indicated that the occurrence of specific
360 species is generally associated with landscape factors depending on their ecological characteristics,
361 such as life stages or growth forms (Akasaka *et al.*, 2010; Raebel *et al.*, 2012; Usio *et al.*, 2014). For
362 example, Raebel *et al.* (2012) showed that dragonflies were associated with landscape factors at long-
363 distance scales, while damselflies were associated with short-distance scales. A possible reason that
364 fish richness was associated with both short- and long-distance scales is that the occurrences of certain
365 species were associated with different spatial scales depending on their dispersal abilities.

366 *4.2 Relative effects of land use and fish abundance on the total phosphorus concentration of farm* 367 *ponds*

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

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

383 In contrast, surrounding vegetation coverage seemed to act as a buffer for eutrophication and
384 sedimentation by suppressing surface run-off through evapotranspiration and filtering the nutrients in
385 the water (Bosch and Hewlett, 1982). In addition, when correlation analyses were performed among
386 landscape variables at a 2,000-m radius, the coverage of broadleaved forest showed a strong, negative
387 correlation with the coverage of urban areas ($r = -0.78$). Likewise, the coverage of grassland at a
388 2,000-m radius showed a moderately high correlation with the coverage of urban areas ($r = -0.66$).
389 Therefore, low coverages of broadleaved forest and grassland are indicators of urbanisation. Urban
390 areas and paddy fields function as sources for non-point pollution (Carpenter *et al.*, 1998). Surface run-
391 off containing rich nutrients from urban and agricultural areas may result in loss of macrophytes,
392 which in turn leads to a turbid state.

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

408 *4.3 Effects of changes in the trophic state on the taxonomic richness patterns of farm pond* 409 *communities*

410 A clear-water state was associated with high taxonomic richness of aquatic plants,
411 macroinvertebrates, and adult Odonata, while a turbid state was associated with high taxonomic

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

423 *4.4 Implications for farm pond management*

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

435 In Europe, conservation of a clear-water state and high vegetation complexity in both existing and
436 newly created farm ponds has been suggested as important in landscapes dominated by cropland,
437 provided that the farmland is extensively managed (Declerck *et al.*, 2006). However, this may not
438 apply in paddy-dominated landscapes in Japan, in which each paddy field is generally small (< 1 ha),
439 extensively managed paddy fields are sporadically distributed, and paddy fields are generally
440 intensively managed at the regional level. Recently, increased attention has been paid to

441 environmentally friendly farming (Usio, 2014). The main reason to implement environmentally
442 friendly farming is to develop multiple functions of farmland beyond their role of producing food (i.e.
443 multi-functionality of agriculture). For this purpose, various environmentally farming practices have
444 been implemented, including wildlife-friendly farming (Usio, 2014). Halving or omitting the use of
445 agrochemicals is the base procedure for all environmentally friendly farming practices. Conservation
446 or restoration of farm ponds within paddy-dominated landscapes may become successful if the
447 arrangement and size of environmentally friendly paddy fields are appropriately considered. For
448 example, environmentally friendly farming may be implemented in a block rather than individually
449 along the area connected by a single agricultural drainage system. In this way, the release of nutrient-
450 rich effluent from paddy fields to agricultural drainage may be mitigated more efficiently.

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

470 through mechanical crayfish removal together with the conservation of carnivorous fish predators (e.g.
471 Japanese eel *Anguilla japonica*, Japanese common catfish *Silurus asotus*) and their habitats.

472 Limitations of our study include its scope and analyses. In Japan, pond managers are generally
473 concerned about the water quality of farm ponds, because pond water is used primarily for irrigated
474 farming. Specifically, more than 54% of all farmland area in Japan comprises rice paddy fields (e-Stat,
475 2017). In rice farming, water quality, together with soil type and diurnal temperature variation, is of
476 primary importance in determining rice grain quality and yield (Hirai *et al.*, 2010). Given that a major
477 focus of farm pond management in Japan is to maintain good water quality, biodiversity patterns in
478 Japanese farm ponds are presumably determined primarily by water quality. Nevertheless, we
479 incorporated water-quality and water management variables to a limited degree in the analyses.
480 Furthermore, the primary focus of agro-ecosystem management is to enhance or secure crop
481 productivity. Therefore, crop productivity may also be a significant determinant of biodiversity
482 patterns in farm ponds. In regions where agricultural drainage is used as a main water source for farm
483 ponds and/or where upper areas are intensively managed as farmland, crop productivity may also
484 influence water quality due to the amount of fertilisers used on farmland. Future studies should
485 encompass productivity indicators together with various water-quality indicators, farming practices,
486 and water management toward a comprehensive understanding of the biodiversity patterns in farm
487 ponds.

488 **5. Conclusions**

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

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507

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647

648 **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

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

Spatial scale	Concentration	Taxonomic richness					
	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

652

653 **Table 3.** Contributions of land-use (i.e. landscape variables and modern pond management), fish
654 abundance, and other environmental variables to the total phosphorus concentration in boosted
655 regression-tree models. The contribution of each variable was assessed by the percentage deviance
656 (D^2) explained after exclusion of each variable from the simplified model. Small letters in brackets (a
657 to f) refer to the labels. Percentage contributions of each land-use variable and fish abundance were
658 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

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

664 **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

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

668

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).

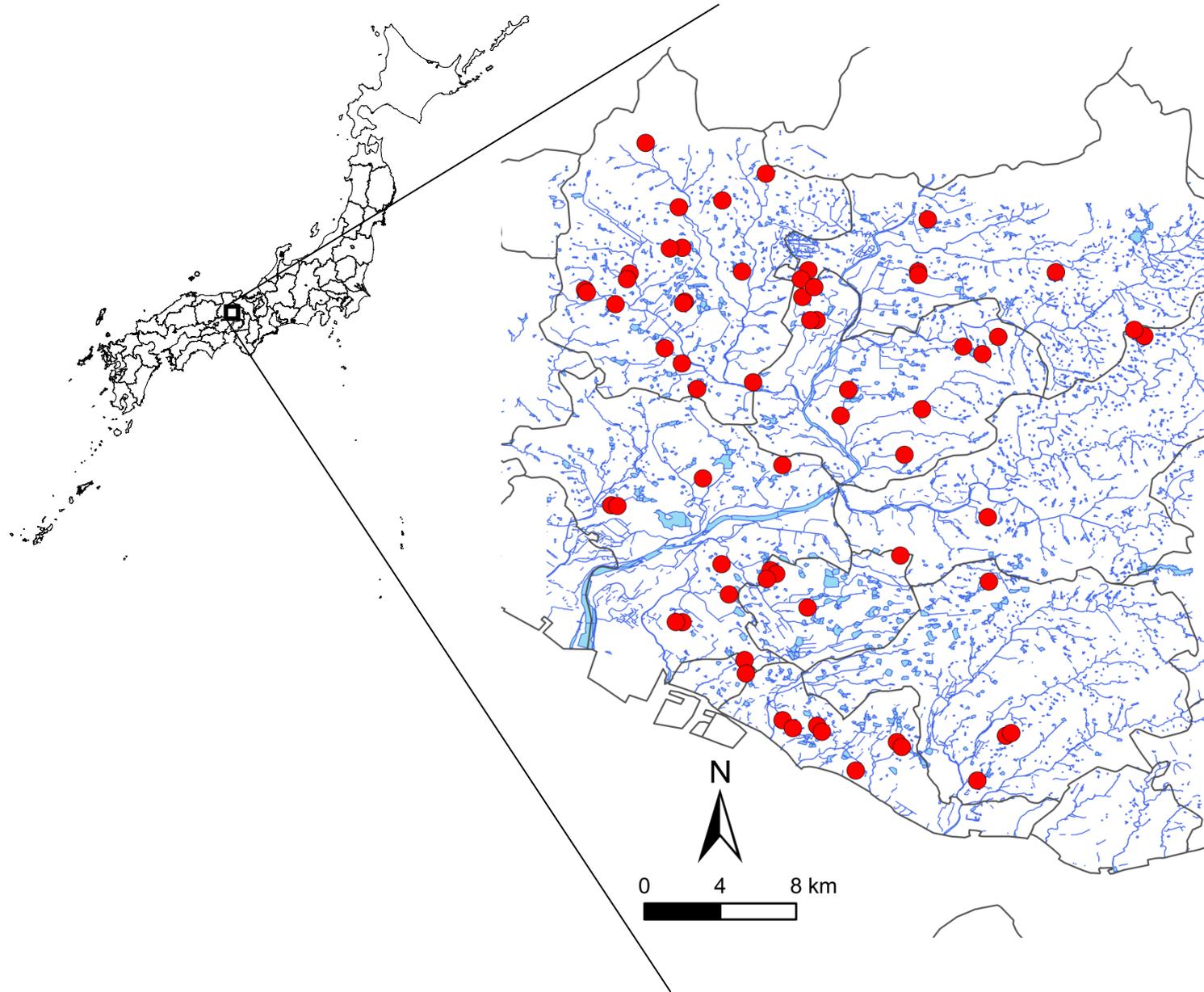


Fig. 1 Usio et al.

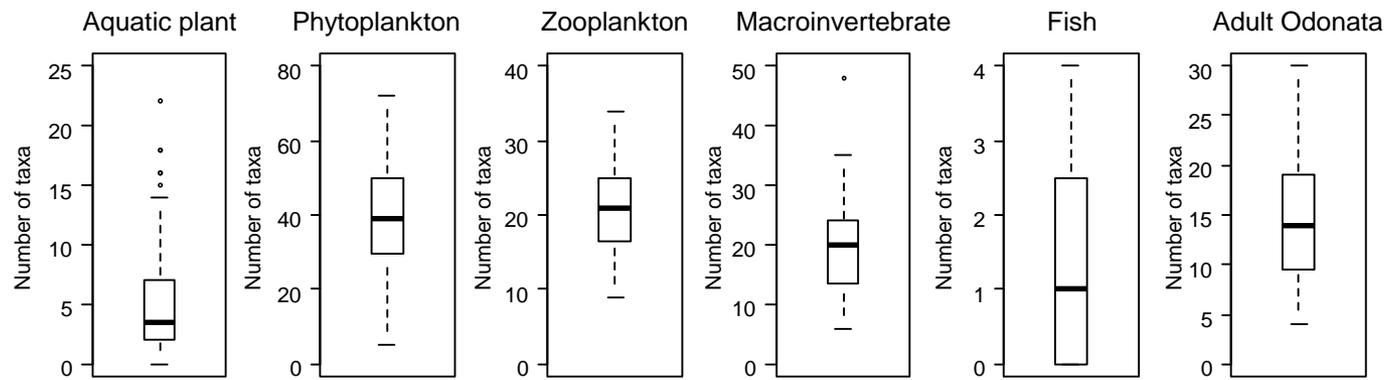


Fig. 2 Usio et al.

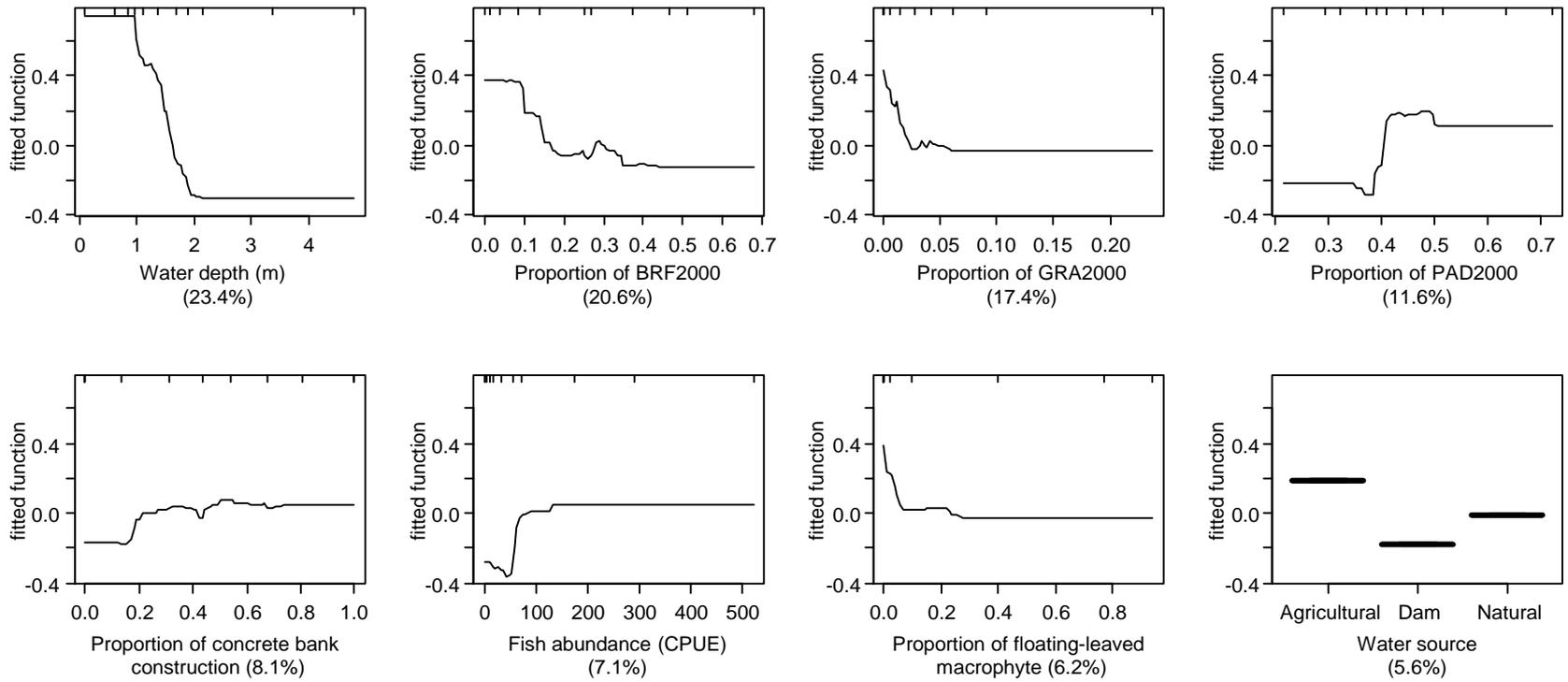


Fig. 3 Usio et al.

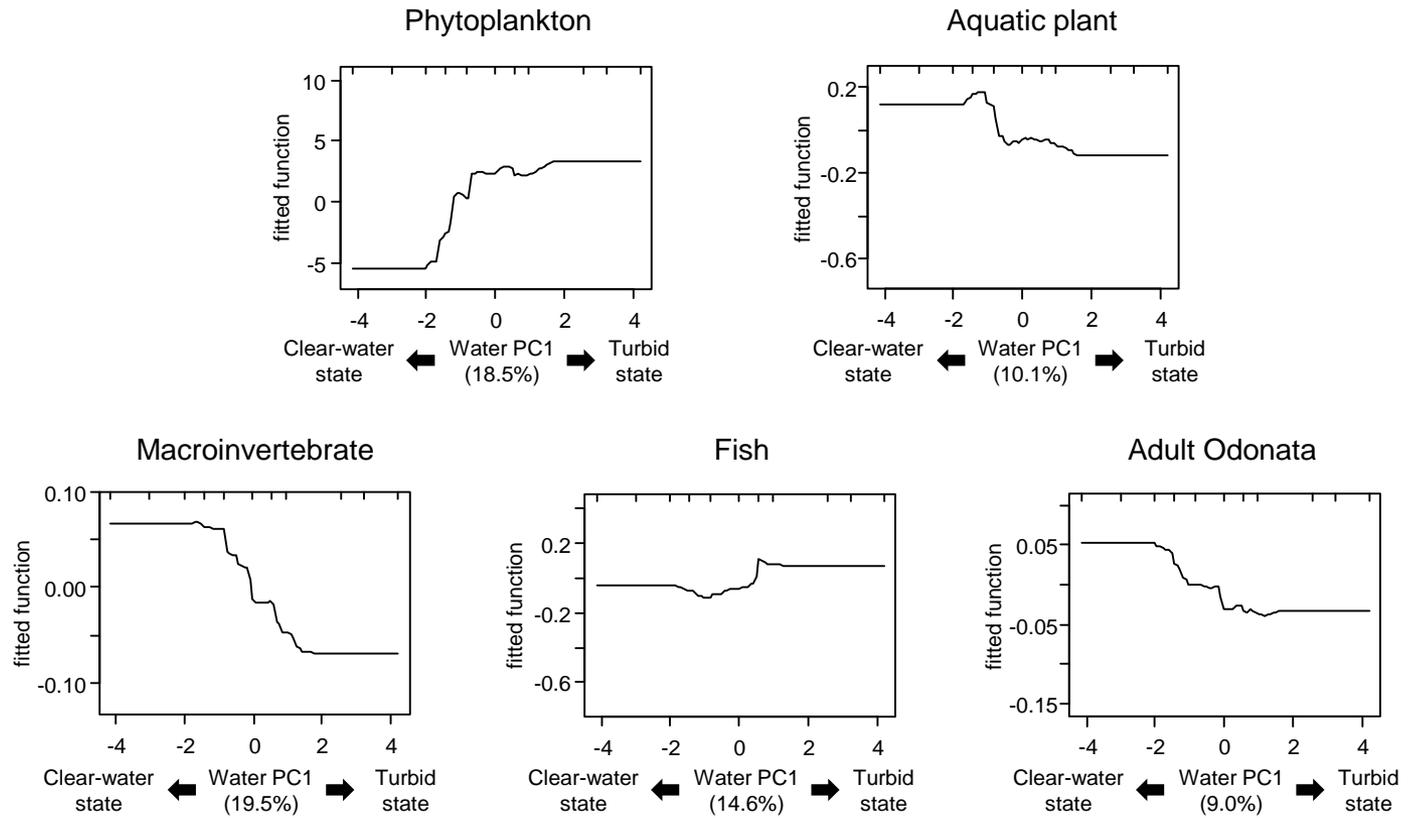


Fig. 4 Usio et al.

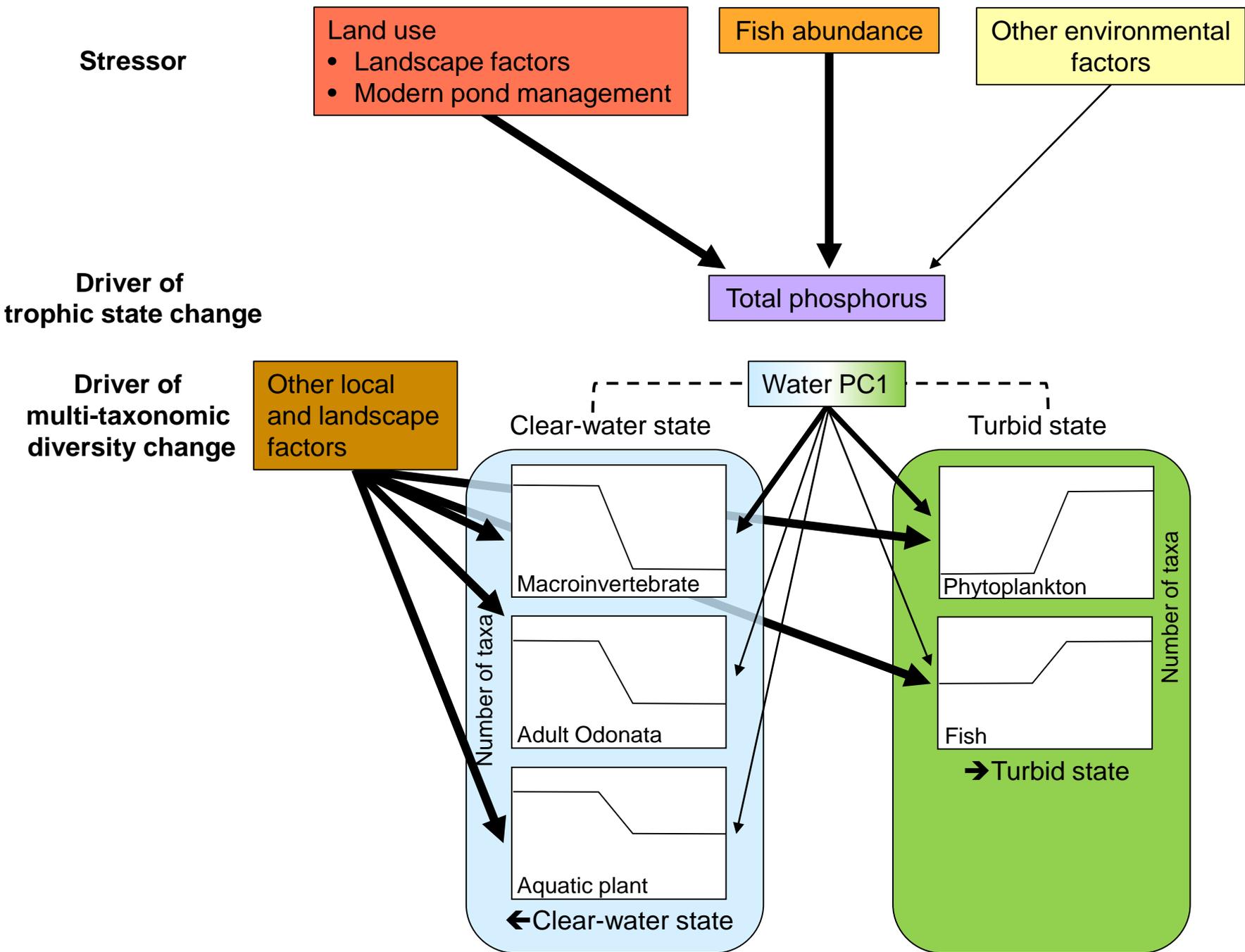


Fig. 5 Usio et al.

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 ($\mu\text{g L}^{-1}$)	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

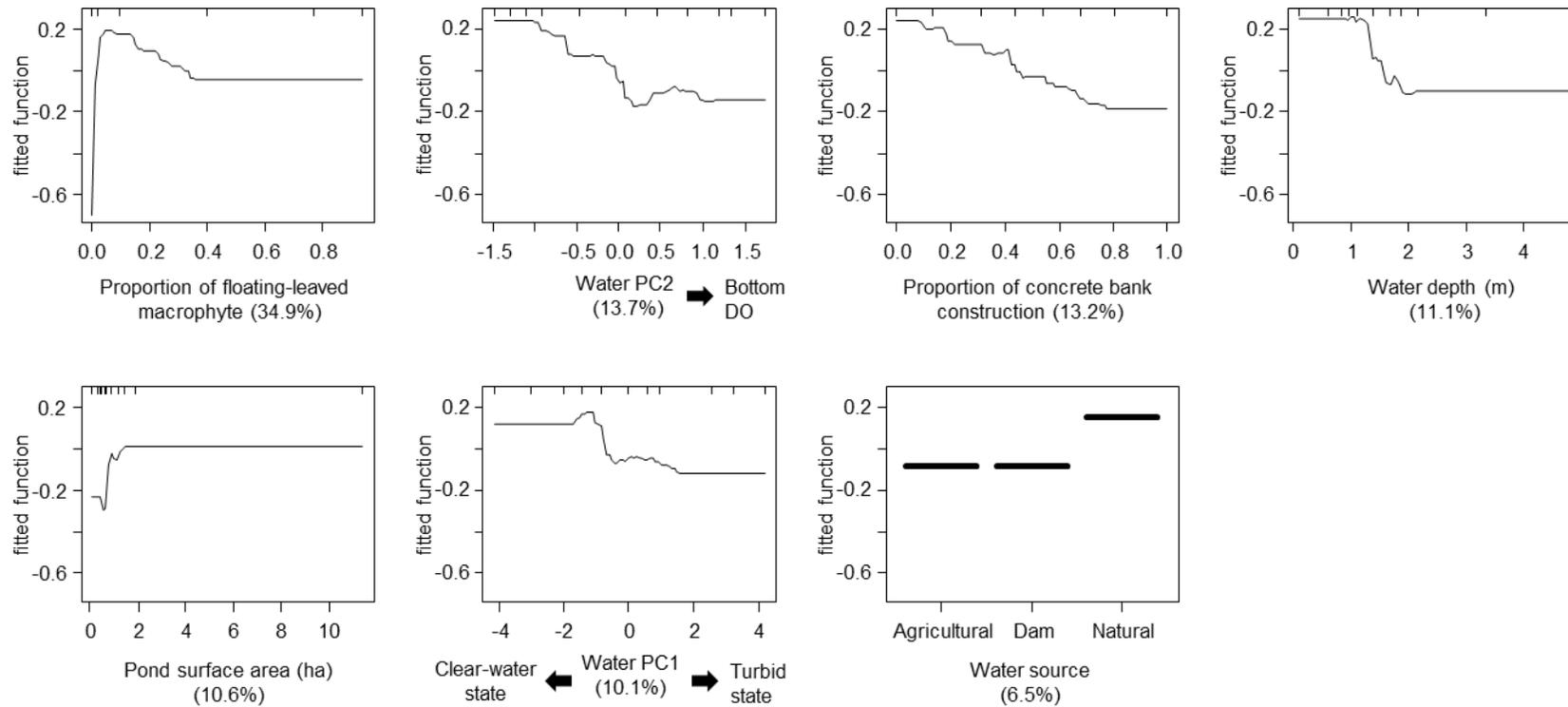


Figure S1. Partial plots of the effects of land-use (concrete bank construction) and other environmental variables on the taxonomic richness of aquatic plants in the simplified, boosted regression-tree model. The fitted function represents the effects of the selected variable on the response variable. 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.