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Contribution of hydrological connectivity in maintaining aquatic plant communities in remnant floodplain ponds in agricultural landscapes.

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Abstract

The expansion of the agricultural landscape has led to the fragmentation of floodplains. These remnant floodplain ponds serve as important habitats for aquatic plants. Hydrological connectivity between floodplain ponds, facilitated by artificial watercourses, plays an important role in providing a migration course for mobile animals, such as fish. However, little is known about the contribution of artificial watercourses to the dispersal of aquatic plants, which are passive dispersers, between floodplain ponds. This study aimed to elucidate the effects of hydrological connectivity through artificial watercourses and environmental factors on the structure and composition of aquatic plant communities in lowland floodplain ponds. Vegetation and environmental surveys of 20 floodplain ponds were conducted in the agricultural landscape of northern Japan. Path analysis was used to clarify the effects of local- and landscape-scale environmental variables on aquatic plant communities with respect to species richness and species coverage. The path analysis results suggested that both hydrological connectivity between floodplain ponds and eutrophication were influential determinants of the species richness of aquatic plant communities. The study findings indicate that water quality management, connectivity conservation, and restoration should be prioritized to maintain aquatic plant communities in degraded floodplain ponds.

Key Words

Dispersal; Hydrochory; Artificial Watercourses; Eutrophication.

Introduction

Wetlands provide habitats for various organisms, such as birds, fishes, and aquatic insects. The total global area of wetlands decreased by 35% from 1900 to 2015 (Ramsar 2018), and the total area of wetlands in Japan decreased by 61% from the 1910s to 1999 (Geographical Information Authority of Japan 2000). Such wetland loss causes habitat reduction and fragmentation, leading to a decline in biodiversity by limiting biological dispersal and genetic exchange (Soons *et al.* 2005; Young *et al.* 1996). A primary cause of wetland loss in Japan is the conversion of wetlands to farmland and residential land (Geographical Information Authority of Japan 2000). Wetlands face serious loss and degradation, especially in lowland floodplains, owing to their suitability for rice cultivation (Fujita 2017).

Aquatic plants found in these habitats include vascular plants, bryophytes, and charophytes, which are adapted to wetland environments and are the primary producers of these wetland ecosystems. Aquatic plants support biodiversity by providing sites for foraging, spawning, and shelter for aquatic organisms and by improving water quality (Kadono 2014). However, aquatic plants are endangered as a result of habitat loss and fragmentation. Approximately 40% of native aquatic plant species in Japan are listed as vulnerable to various environmental changes (Ministry of the Environment Government of Japan 2015).

Establishing new habitats and ensuring gene pool interaction through propagule dispersal are essential to conserve aquatic plant communities (Middleton *et al.* 2006). The propagules of aquatic plants can be dispersed by wind (anemochory), animals (zoochory), and water (hydrochory) (Middleton *et al*. 2006). Because free-floating, submerged, and floating-leaved plant species inhabit highly water-dependent environments, the propagules of several of these species are adapted to hydrochory and hydrological connectivity promotes their dispersal (Akasaka *et al*. 2011; Bolpagni *et al.* 2020; Dahlgren & Ehrlen 2005). Hydrochory also promotes secondary dispersal, allowing propagules to be transported farther (Soomers *et al*. 2013). Considering these ecological roles, conserving hydrological connectivity is important for the dispersion of aquatic plants.

Floodplain ponds are important habitats for aquatic plants because of the high species diversity of aquatic plants compared to other water bodies (e.g., rivers and large lakes) (Geest *et al*. 2003; Sun *et al.* 2022). In floodplain ponds, flooding allows dispersal between ponds, and regular disturbances create new habitats (Geest *et al*. 2003). However, the frequency of flooding has decreased owing to the effects of land use conversion and river channelization, hampering aquatic plant dispersal (Opperman *et al*. 2010). Hydrological connectivity through artificial watercourses, such as agricultural canals and road drainage canals in lowland areas, plays an important role in providing migration courses for mobile animals, such as fish (Ishiyama *et al*. 2014, 2015). However, little is known about the contribution of artificial watercourses to the dispersal of aquatic plants between floodplain ponds and the effect of connectivity on the structure and composition of the aquatic plant community.

The structure and composition of aquatic plant communities are influenced by a variety of factors in their physical environment, such as water depth (Sakurai *et al*. 2017), water surface area (Geest *et al*. 2003; Akasaka & Takamura 2012), turbidity (Janne *et al*. 2013), water temperature (Lacoul & Freedman 2006), water level fluctuations (Lacoul & Freedman 2006), sediment (Ikushima 1972), and water quality parameters, such as pH, electrical conductivity, and nutrient concentration (Takamura *et al*. 2003; James *et al*. 2005). In particular, in areas where the land use type has changed, eutrophication progresses faster than it does under natural conditions as a result of nutrient loading caused by human activities in agricultural and urban areas (Lisa & Carolyn 2007). As eutrophication progresses, only plants tolerant to eutrophication survive, resulting in a decrease in aquatic plant diversity (Takamura *et al*. 2003; James *et al*. 2005). In addition, phytoplankton blooms lead to an increase in the turbidity of the water column, affecting the light environment and inhibiting the growth of aquatic plants, especially those that are submerged (Matthew *et al.* 2018).

This study aimed to elucidate the effects of hydrological connectivity provided by artificial watercourses, water quality, and physical environments on the structure and composition of aquatic plant communities (that is, species richness and species coverage) in lowland floodplain ponds. In this study, we considered water quality and physical environments in addition to hydrological connectivity for our analyses because knowledge of the relative importance of each factor is essential to develop effective conservation measures.

Materials and Methods

Study site

In this study, a total of 20 floodplain ponds were surveyed in the Tokachi region, including Ikeda and Toyokoro towns, in northern Japan (42° 78' 60"–90' 27" N, 143° 42' 82"–59' 82" E). The average annual temperature in this region is 5.8 °C, and the average annual precipitation is 869.7 mm (1981–2020 average: Japan Meteorological Agency 2019). The floodplain ponds are located in the lower part of the Tokachi River, and the surface area of the ponds ranges from approximately 0.1 to 13.6 ha. The surrounding landscape is dominated by farmlands, such as croplands and pastures (Fig. 1; Fig. 2). Many floodplain ponds are interconnected through agricultural ditches. Historically, several floodplain ponds were distributed along the meandering main watercourses of the lower Tokachi River. In the 1880s, however, the Tokachi River was straightened as a flood control measure, and most protected inland areas along the river were converted to cities and farmlands (Okuyama & Fujomaki 2001). Consequently, overbank flooding rarely occurred in the study region. We used aerial photographs to determine whether the floodplain ponds surveyed in this study are remnant floodplain ponds or those created as a result of river channelization (Geographical Survey Institute 2020). For the surveys, floodplain ponds were randomly selected by considering a wide range of variations in the area of floodplain ponds and the degree of hydrological connectivity (isolated or connected by agricultural ditches). See Supplementary Table 1 for the range of environmental gradients of the floodplain pond in the study area.

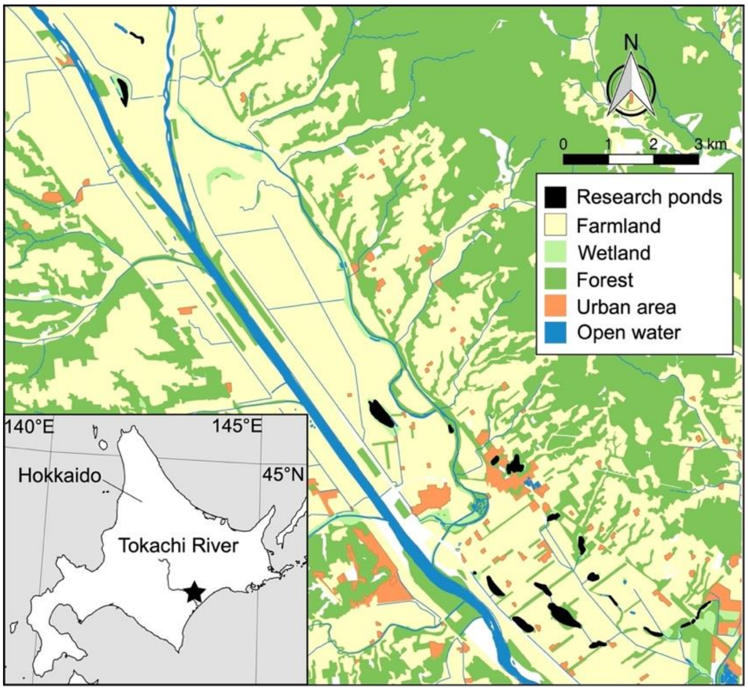


Fig. 1. Map of the study site. The star symbol represents the location of the study region. Agricultural ditches are indicated as open water and represented by a thin straight line.

Fig. 2. A typical floodplain pond within the study area. The floodplain ponds are surrounded by farmland. Other photographs of researched floodplain ponds are included in Supplementary Figure 1.

Vegetation survey

A vegetation survey was conducted once in each floodplain pond within the period from July to September 2018–2019, when the aquatic plants were thriving. A total of 30 quadrats (2 m × 2 m) were randomly set on the surface of each floodplain pond and the species names and coverage (in 5% increments) of the aquatic plants that appeared in the quadrats were recorded. Free-floating, submerged, and floating-leaved plants, which are frequently dispersed through hydrochory, were targeted during the survey (Dahlgren & Ehrlen 2005). A boat or floater was used to conduct the vegetation surveys. Submerged plants were identified visually if the stems and leaves extended close to the surface of the water. If the plant body was deeply submerged and not clearly visible, the submerged plant was collected by hooking up with a rope and identified. The coverage of deeply submerged vegetation was measured by looking through underwater glasses. Based on the results of the vegetation survey, the total number of aquatic plant species and the average coverage over 30 quadrats were calculated for each aquatic species in each floodplain pond. Species were identified using Kadono (2008, 2014) as reference.

Environmental factors

Local- and landscape-scale environmental variables were selected to explain the structure and composition of the aquatic communities (that is, species richness and species coverage). Local-scale environmental variables were measured at the same time as the vegetation survey, and landscape-scale environmental variables were obtained from the National Land Numerical Information (Geographical Information Authority of Japan 2005) and 1:25,000 scale vegetation map GIS data (Ministry of Environment 2017).

The local-scale environmental variables were the physical environment (water depth, water depth variation, area of water surface, and turbidity) and nutrient level (dissolved total nitrogen (DTN) and dissolved total phosphorus (DTP) concentrations). For each quadrat in each floodplain pond, water depth and turbidity were measured using aluminum staff and a multi-item water quality meter (WQC-24, DKK-TOA Co., Ltd., Tokyo, Japan), respectively. The average values of these measurements for each floodplain pond were used as local-scale variables. The water depth variation in each floodplain pond was calculated as the standard deviation of the measured water depth. The water surface area of each floodplain pond was calculated using the data available from the National Land Numerical Information (Geographical Information Authority of Japan 2005) using QGIS. To analyze DTN and DTP, surface water was collected at five locations per floodplain pond, and the samples were immediately filtered using glass fiber filter paper (0.7 μm, GF/F, GE Healthcare, Chicago, the United States). The sample filtrate was transferred to the laboratory and stored at -18 °C until further analysis. Subsequently, DTN and DTP in the filtrate were analyzed using a flow-injection analyzer (AACS-4, BL-TEC Inc., Osaka, Japan).

Landscape-scale environmental variables included the connectivity of watercourses and land use ratio around the floodplain ponds. Connectivity was represented by the decrease in the integral index of connectivity (dIIC). The dIIC considers one habitat as a connecting element between other habitats. It can also be calculated without knowing the coefficient of dispersion, which is specific to the target species (Baranyia *et al.* 2011). The dIIC was calculated as follows:

$$IIC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j/(1+nl_{ij})}{{A_L}^2}$$

$$dIIC_k = \frac{IIC - IIC_{remove,k}}{IIC} \times 100$$

where i and j represent any floodplain pond combination, a_i represents the area of floodplain pond i, A_L represents the total area of all floodplain ponds, and nl_{ij} represents the number of links in the shortest paths between floodplain ponds i and j.

The IIC represents the connectivity of floodplain ponds as an entire landscape (all floodplain ponds along the lower Tokachi River). The value of $dIIC_k$ represents the percentage reduction in the IIC that occurs when wetland k is lost (that is, the importance of wetland k in the entire floodplain pond network); floodplain ponds with larger $dIIC_k$ values contribute more toward maintaining the network. The dIIC can be calculated based on the length of the watercourses, assuming that the floodplain ponds are functionally connected. This length is called the threshold distance and can be set on the basis of the territory and dispersal distance of living organisms (Baranyia *et al.* 2011). However, the dispersal distance of aquatic plants through the watercourses in the study area is unknown. Therefore, based on the studies conducted by Ishiyama *et al.* (2014, 2015, 2020), the threshold distances were determined to be 0.5, 1, 3, 5, 7.5, 10, 12, and 14 km. To evaluate the importance of connectivity exclusively through the watercourses, the distances were set as less than or equal to 14 km, which did not include the main river channel. The dIIC was calculated using Conefor 2.6 software (Saura & Torné, April 2012).

The percentages of farmland, urban, and farmland + urban areas around the floodplain pond were calculated for the analyses, as we assumed that the land use around the studied floodplain ponds would affect the nutrient conditions in the water. The outer buffers by stage were determined as 10, 50, 100, 500, and 1000 m from the pond edge to detect the most influential spatial scale for each of DTN and DTP. Prior to that, we used the data obtained by extracting and reclassifying the corresponding land use from 1:25000 scale vegetation map GIS data (Ministry of Environment 2017). We used QGIS (version 2.18.24) for all GIS analyses. The environmental variables were subjected to natural logarithmic transformation to improve normality and standardized to make different units comparable.

Data analysis

Path analysis was used to investigate the factors affecting aquatic plant communities in the surveyed areas. Parameter estimates for the path analysis were determined based on the maximum likelihood method using structural equation modeling (Fan *et al.* 2016; Shipley 2016). The species richness and coverage ratio for each aquatic plant species were used as the objective variables (Fig. 3). The explanatory variables were selected from the following 29 environmental factors. The landscape-scale variables were dIIC (0.5, 1, 3, 5, 7.5, 10, 12, and 14 km) and land use (farmland, urban, farmland + urban ratios for 10, 50, 100, 500, and

1000 m buffers). The local-scale variables were the nutrient level (DTN and DTP) and physical environment information (water depth, water depth variation, turbidity, and area). However, ‘water depth variation’ was used only to explain the species richness of aquatic plants because we hypothesized that variation in depth should explain overall species richness rather than coverage of individual species. Owing to the small sample size (n = 20), all variables included in this study could not be analyzed. The fully developed path analysis model consisted of one variable from the dIIC, 1–2 variables from land use, and 0–1 variable from the physical environment categories based on our sample size. Subsequently, the path analysis was run by swapping one variable for each category (1–2 for land use, 0–1 for physical environments) to detect the model with the highest fitting degree (that is, lowest Akaike's information criteria). We described the scientific rationale and limitations of the environmental variables used in the path analysis in Table 1. Each variable was used in the path analysis with the expectation that it would directly or indirectly affect the aquatic plant community. Due to the small sample size (n=20), we could not examine all the possible relationships among variables in this model (e.g., the relationship between land use and the physical environment and other water quality variables such as chlorophyll concentration). Model fitting was also checked with the RMSEA (root mean square error of approximation) < 0.06. The software R ver. 3.5.1 (R Core Team 2018) and the lavaan package ver. 0.6–5 (Rosseel 2019) were used for the analysis.

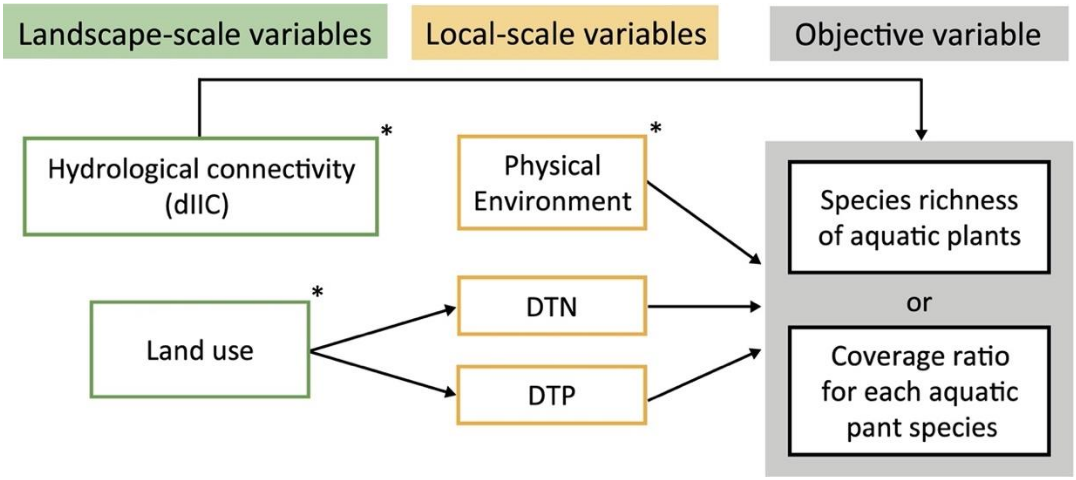


Fig. 3 The model for path analysis. The arrow indicates the expected direction of influence.

*Boxes with asterisks indicate categories where a reduced number of variables were selected. We selected one variable from the dIIC (0.5, 1, 3, 5, 7.5, 10, 12, and 14 km), 1–2 variables from land use (farmland, urban, farmland + urban ratios for 10, 50, 100, 500, and 1000 m buffers), and 0–1 variable from the physical environment categories (water depth, water depth variation, turbidity, and area) by considering all combinations of variables.

Table 1 Scientific rationale and limitation of environmental variables for path analysis (Figure 3)

Environmental variables	**Scientific rationale and limitation**
Hydrological connectivity (dIIC)	We examined the effect of hydrological connectivity on 'species richness of aquatic plants' and 'coverage ratio for each aquatic plant species', which may be affected differently depending on the hydrochory (or dependence on hydrochory) ability of the aquatic plant species (Akasaka *et al.* 2011; Coetzee *et al.* 2009; Smits *et al*. 1989). Hydrological connectivity may indirectly affect aquatic plant communities through the physical environment and water quality (e.g., nutrient inputs from connected watercourses), but we did not consider the pathway in this study.
Land use	We examined effect of land use, such as farmland and urban, on aquatic plant communities through water quality (Egemose & Jensen 2009; Lee 1973; Jeppesen *et al.* 2000). Land use could also affect the physical environment, such as water turbidity, but we did not consider the pathway in this study.
Physical Environment	We examined general physical environment parameters that could have a direct influence on aquatic plant communities (Sakurai *et al.* 2017; Geest *et al.* 2003; Akasaka & Takamura 2012; Janne *et al.* 2013). We hypothesized that 'variation in depth' should explain overall species richness rather than coverage of individual species.
DTN, DTP	We examined direct effects of nutrients such as DTN and/or DTP on aquatic plant communities. We expected nutrient concentrations to be a major influential factor because each species of aquatic plants has a different level of tolerance to eutrophication (Takamura *et al.* 2003; James *et al.* 2005).

Results

Eight submerged species, five floating-leaved species, and seven free-floating species were identified through the surveys (a total of 20 species; Table 2; Supplementary Tables 1 and 2). The sampling effort applied in this study is sufficient to reveal the community structure of aquatic plants, which is verified by rarefaction and extrapolation curves (Colwell *et al.* 2012). See Supplementary Figure 2 for details. Two species in the study area with highly similar morphology, *Lemna minor* and *Lemna aoukikusa*, could not be identified in the field; these species were collectively categorized as *Lemna* sp. for the analysis.

The species richness of aquatic plants in each floodplain pond was directly influenced by the dIIC and DTP in the path analysis (Fig. 4-1). We conducted variable selection and obtained a threshold distance of 3 km for the connectivity index dIIC (Supplementary Tables 3 and 4). Model estimates indicated that a higher dIIC supported a greater number of species. The urban ratio within a 100 m buffer was selected as an indicator of land use. The results showed that urbanization caused nutrient enrichment, which decreased species richness. For the estimated values that had a significant effect on the number of species, the standardized path coefficient was larger for the DTP than for dIIC. Neither the physical environment nor DTN had a significant effect on the number of species. The DTP and DTN values were in the range of 0.01-1.18 mg L^{-1} and 0.35-9.21 mg L^{-1}, respectively (Table 3).

Among the 20 target species, the coverage of nine aquatic plants (*Nuphar japonica*, *Nymphaea tetragona*, *Hydrilla verticillata*, *Potamogeton natans*, *P. octandrus*, *P. maackianus, P. compressus*, *Ceratophyllum* *demersum*, and *Utricularia* × *japonica*) was successfully represented by path analysis (p<0.01) (Supplementary Tables 3 and 4). Out of these nine species, seven unique species were selected and similar analysis results were obtained; based on the results, these species were classified into three groups according to the relative influence of dIIC for discussion: (A) *N. japonica*, *N. tetragona, P. natans*, *C. demersum* and *H. verticillata*, which were positively influenced by dIIC (Fig. 4-2-A). (B) *U.* × *japonica*, which was negatively influenced by dIIC (Fig. 4-2-B). (C) *P. octandrus*, *P. maackianus* and *P. compressus*, which were unaffected by dIIC and water quality (Fig. 4-2-C).

Table 2. Characteristics of aquatic plants found during the vegetation survey conducted in floodplain ponds. **Ceratophyllum demersum* L. includes the possibility of *C. platyacanthum* Cham. subsp. *oryzetorum* (Kom.) Les. *'Turion' (in the propagule column) refers to an asexual reproductive organ that is a unique feature of aquatic plants and is formed at the tip or side of the stem. 'Fragments' indicates the ability of the plant to regenerate from fragments. Propagule types mentioned in parentheses occur infrequently. The list is based on the following references: Agami & Waisei (1988), Capers *et al.* (2010), Coetzee et al. (2009), Hamashima (2008), James *et al.* (2005), Kadono (1984, 2007, 2008, 2014), Keddy (1976), Matsumoto (1981), Ministry of the Environment Government of Japan (2015), Shimoda and Hashimoto (1993), Smits *et al.* (1989), Szalontai *et al.* (2018) and Van Den Berg *et al.* (1999).

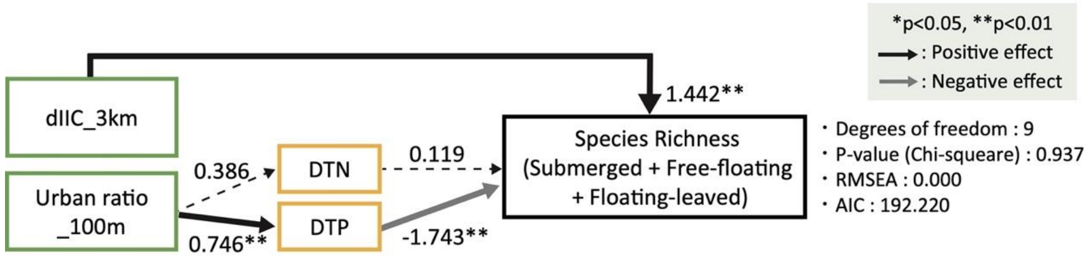
Species	**Life form**	**Red List (Japan)**	**Lifespan**	**Resistance to eutrophication**	***Propagule**	**Grouping by path analysis results**
Nuphar japonica DC.	floating-leaved	-	perennial	mid	seed	A
Nymphaea tetragona Georgi var. *erythrostigmatica* Koji Ito	floating-leaved	VU	perennial	low-mid	seed	A
Brasenia schreberi J.F.Gmel.	floating-leaved	-	perennial	low-mid	seed,turion	-
Potamogeton natans L.	floating-leaved	-	perennial	mid	seed, turion	A
Trapa japonica Flerow	floating-leaved	-	annual	high	seed	-
Utricularia × japonica Makino	free-floating	NT	perennial	low-mid	trion, fragments	B
Lemna aoukikusa Beppu et Murata subsp. *aoukikusa*	free-floating	-	annual	high	seed	-
Lemna minor L.	free-floating	-	perennial	high	(seed), frond	-
Lemna trisulca L.	free-floating	VU	perennial	low	(seed), frond	-
Spirodela polyrhiza (L.) Schleid.	free-floating	-	perennial	high	(seed), frond	-
**Ceratophyllum demersum* L.	free-floating	-	perennial	high	seed, turion, fragments	A
Riccia fluitans L.	free-floating	NT	perennial	NA	spore, frond	-
Hydrilla verticillata (L.f.) Royle	submerged	-	perennial	high	(seed), turion, fragments	A
Potamogeton octandrus Poir. var. *octandrus*	submerged	-	perennial	mid	seed, turion	C
Potamogeton maackianus A.Benn.	submerged	-	perennial	high	seed, fragments	C
Potamogeton compressus L.	submerged	-	perennial	high	seed, turion	C
Potamogeton pectinatus L.	submerged	NT	perennial	mid-high	seed, turion	-
Najas marina L.	submerged	-	annual	NA	seed	-
Najas minor All.	submerged	VU	annual	NA	seed, fragments	-
Myriophyllum verticillatum L.	submerged	-	perennial	low	seed, turion, fragments	-

Table 3. Environmental characteristics of the study sites.

The nephelometric turbidity unit (NTU) was used to measure turbidity at the study sites using the formazin standard solution. DTN and DTP indicate the dissolved total nitrogen and dissolved total phosphorus concentrations, respectively. The dIIC (decrease in the integral index of connectivity) is an index representing the connectivity of water courses for each floodplain pond. The number that follows the dIIC represents the threshold distance used to calculate connectivity. The farmland, urban, and farmland + urban ratios around the floodplain pond were calculated. The outer buffers for the land use calculation by stage were determined to be 10, 50, 100, 500, and 1000 m.

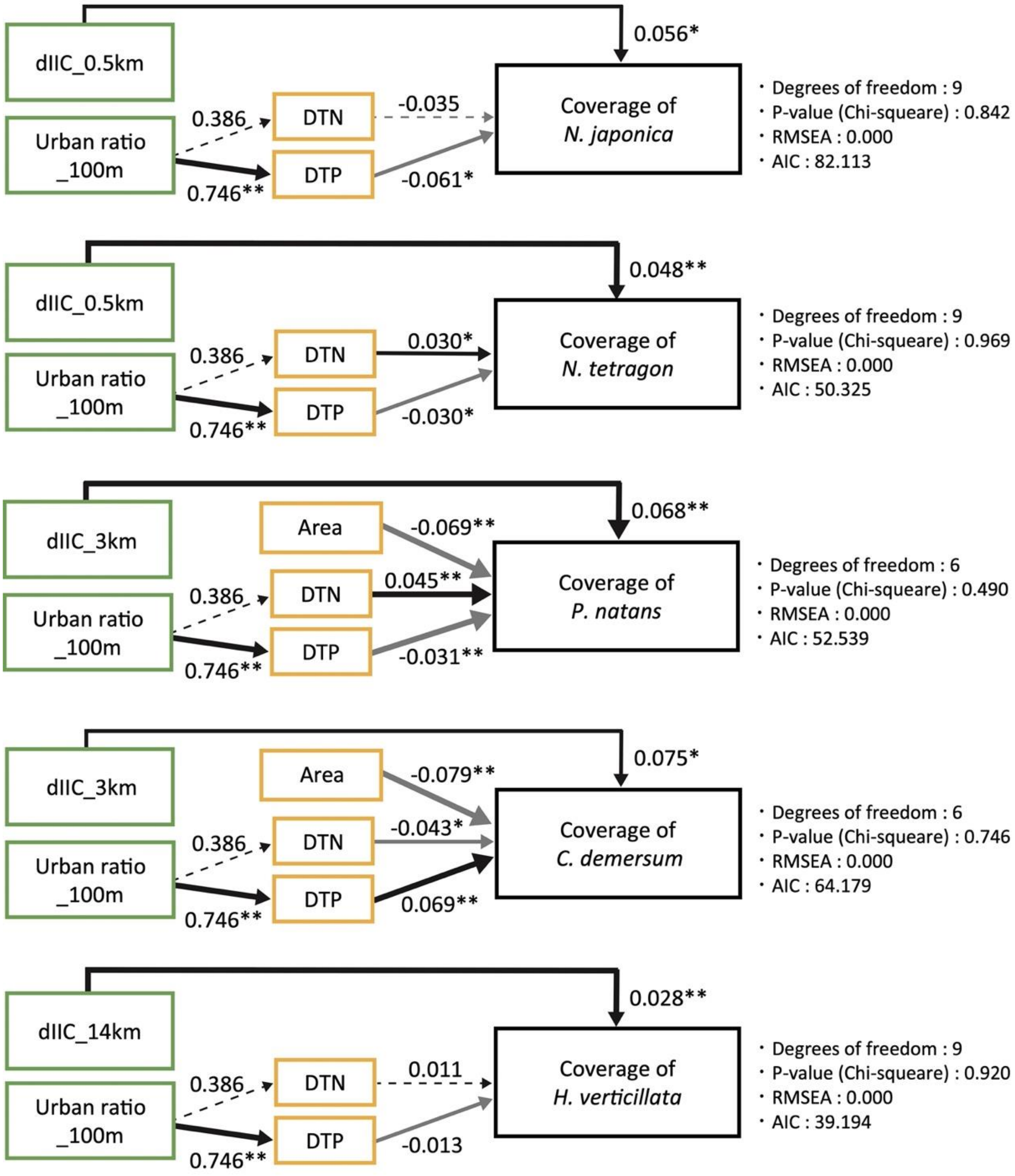
	Turbidity (NTU)	Depth (cm)	Depth variation (cm)	DTN (mg L^{-1})	DTP (mg L^{-1})
median	9.46	108.33	27.79	1.35	0.02
min	3.69	46.13	5.30	0.35	0.01
max	55.11	192.67	68.71	9.21	1.18
	Area (m^2)	dIIC_0.5km	dIIC_1km	dIIC_3km	dIIC_5km
median	20006.58	0.43	0.54	2.66	3.02
min	1202.48	0.00	0.00	0.00	0.00
max	135768.18	28.52	32.48	37.91	40.31
	dIIC_7.5km	dIIC_10km	dIIC_12km	dIIC_14km	
median	3.10	1.88	1.88	1.77	
min	0.00	0.00	0.00	0.00	
max	37.00	35.25	34.38	35.54	
Farmland ratio	_10m (%)	_50m (%)	_100m (%)	_500m (%)	_1000m (%)
median	8.40	26.41	48.57	77.57	72.03
min	0.00	0.00	0.00	25.12	44.29
max	96.32	98.31	98.38	98.54	91.33
Urban ratio	_10m (%)	_50m (%)	_100m (%)	_500m (%)	_1000m (%)
median	0.00	0.00	0.00	1.29	3.19
min	0.00	0.00	0.00	0.00	0.71
max	41.00	50.94	67.41	37.25	17.04
Farmland + Urban ratio	_10m (%)	_50m (%)	_100m (%)	_500m (%)	_1000m (%)
median	14.69	28.59	51.44	79.62	75.73
min	0.00	0.00	1.85	27.06	59.23
max	96.32	98.31	98.38	98.54	95.12

1) Result of path analysis where the objective variable is species richness of aquatic plants.



2) Result of path analysis where the objective variable is coverage ratio for each aquatic plant species.

2-A) Species positively affected by dIIC.



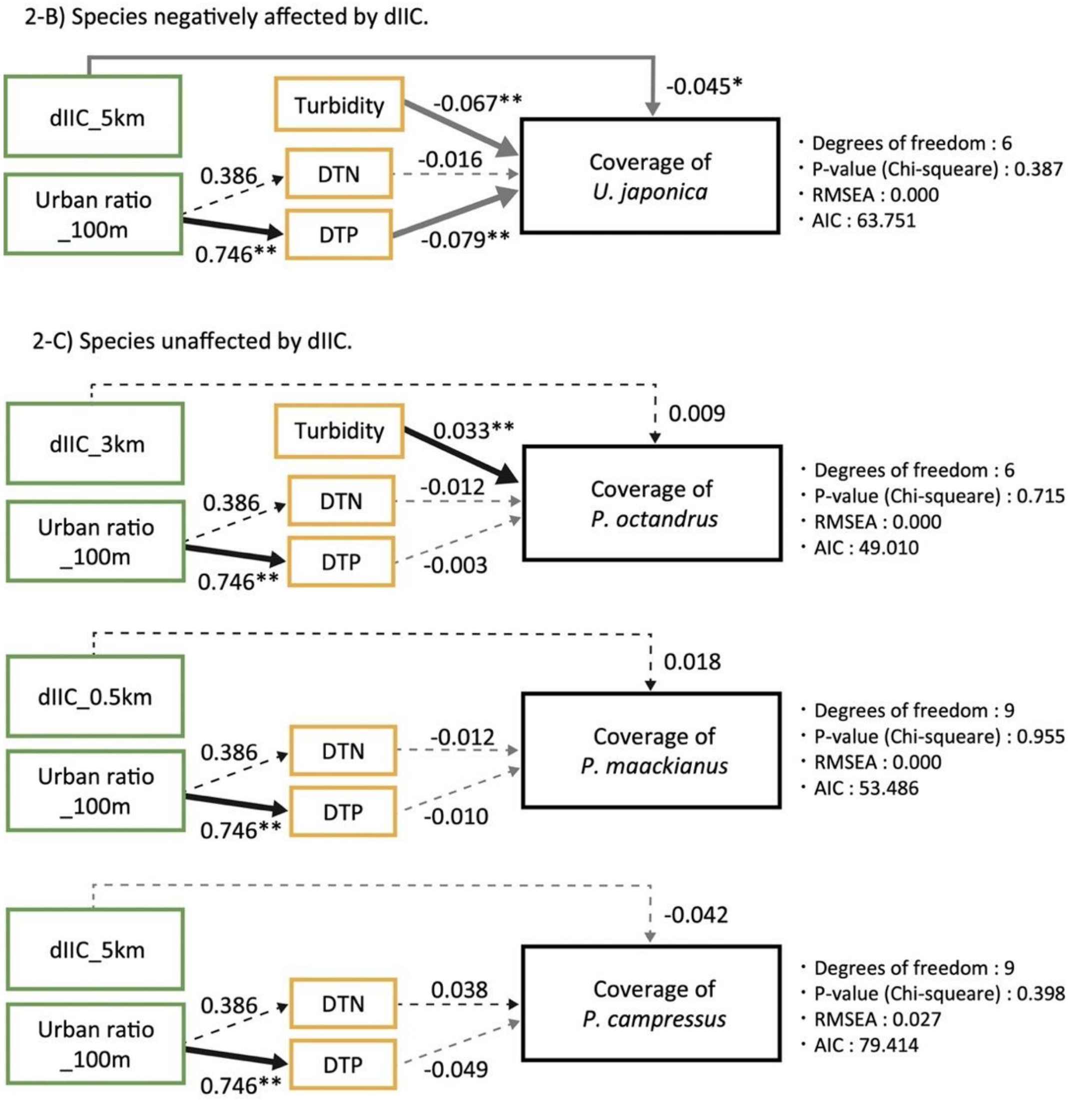


Fig. 4 Results of the path analysis depicting the direct and indirect effects of hydrological connectivity, land use, and local habitat quality on the species richness and coverage of endangered aquatic plants. The numbers indicate the standardized path coefficients estimated using the maximum likelihood method. Thick lines indicate significant paths with *p*<0.01, thin lines indicate significant paths with *p*<0.05, and thin dashed lines indicate no statistical significance. Black and gray lines show the positive and negative effects, respectively.

Discussion

Effect of hydrological connectivity and local environments on species richness

We found that hydrological connectivity between floodplain ponds was suggested to be a significant determinant of the species richness of aquatic plant communities. The path analysis results that the species richness increased with increasing dIIC_3 km in the study area (Fig 4-1). This indicates that watercourse connectivity increases the chances of propagule supply (Akasaka *et al.* 2012). Even at low velocity, wind can move propagules over the water surface (Soomers *et al.* 2013), and heavy rainfall can temporally promote dispersal. Therefore, we believe that hydrological connectivity through watercourses increases the likelihood of dispersal for aquatic plants. As emphasized in this study and in previous studies (Akasaka *et al.* 2012; Bolpagni *et al.* 2020; Ishiyama *et al.* 2014, 2015; Soomers *et al.* 2013), watercourses in lowland floodplains can be important dispersal pathways for aquatic plants. The path analysis selected 3 km as the threshold distance for the dIIC, which implies that 3 km can be regarded as the comprehensive dispersal distance encompassing all aquatic plants in the study region.

The path analysis results for species richness suggested that DTP directly decreased species richness in the study area (Fig. 4-1). In fact, DTP was affected more by the urban ratio than by the farmland ratio and had a significant positive correlation with the urban ratio_100 m buffer in this area. Previous studies have shown that phosphorus discharged from residential lands and industrial areas causes eutrophication by supplying nutrients to floodplain ponds (Egemose & Jensen 2009; Lee 1973), which results in a reduction in the number of aquatic plant species that can survive in these ponds (Jeppesen *et al.* 2000). It has also been shown that land use (especially urban) at a 100 m scale more strongly affects water quality than that at larger landscape scales in summer when dissolved nutrients are concentrated by evaporation of pond water (Kuranchie *et al.* 2022; Zhang *et al.* 2019). The sewerage penetration rate (number of households equipped with sewerage systems among the total households in the town) in the study area was 86.0% in Toyokoro Town and 72.2% in Ikeda Town as of 2019 (Ikeda Town Hall 2021, Toyokoro Town Hall 2022). The specific source of nutrient runoff in the urban area in this study site is not well understood; however, identifying the source and taking appropriate measures is necessary to prevent eutrophication of floodplain ponds. In contrast to DTP, DTN did not affect species richness. In the study region, more than half of the surveyed ponds exceeded the baseline for eutrophication, that is, over 1 mg L^{-1} of TN, which is defined as the minimum level that is not considered unpleasant in the daily lives of citizens (Level 5) (Ministry of the Environment Government of Japan 2019). Even in the study sites, where the extent of eutrophication was below Level 5, the variation in DTN was small. However, there was a large variation in DTP below Level 5 (TP of 0.1 mg L^{-1}) among the study sites. This indicates that phosphorus, rather than nitrogen, may be a major factor regulating eutrophication in this area (Jeppesen *et al.* 2000). However, this result is derived from the assumption that the hypothetical paths encompass the conditions necessary for the establishment of aquatic plants in this region, and further studies are needed to elucidate other cause-and-effect relationships among the environmental variables that we could not consider in this study.

Effects of hydrological connectivity and local environments on each species

The path analysis results for group A suggested that the coverage of *N. japonica* and *N. tetragona* was positively affected by dIIC_0.5 km, that of *P. natans* and *C. demersum* was positively affected by dIIC_3 km, and that of *H. verticillata* was positively affected by dIIC_14 km in the study area (Fig. 4-2-A). *N. japonica* and *N. tetragon* reproduced exclusively through seeds. These species might be unsuitable for zoochory because the seeds of related species (*Nuphar lutea* and *Nymphaea alba*) are easily digested by birds and fish and are vulnerable to drying (Smits *et al.* 1989). A minimum scale of 0.5 km was selected as the dIIC threshold distance, thus confirming that *N. japonica* and *N. tetragon* have poor dispersal ability and depend on hydrochory (Smits *et al.* 1989).

Hydrological connectivity between habitats may aid in the dispersal of hydrochory-specific species, as previously emphasized (Akasaka *et al.* 2012; Bolpagni *et al.* 2020; Ishiyama *et al.* 2014, 2015; Soomers *et al.* 2013). Among Group A species, *H. verticillate, P. natans* and *C. demersum* can be easily propagated through turions and fragments. These characteristics make *H. verticillata* an invasive alien species in North America and *C. demersum* in New Zealand (Umetsu *et al*. 2012; Global Invasive Species Database 2022). Of the three species, *H. verticillata* has a high ability to regenerate from fragments (Umetsu *et al.* 2012) and has expanded its distribution by attaching fragments to recreational boats and moving in running water (Coetzee *et al*. 2009). In addition, turions and fragments of related species of *P. natans* (*Potamogeton* *crispus* and *Potamogeton richardsonii*) and *C. demersum* are drought tolerant to some extent (Barnes *et al.* 2013; Heidbuchel *et al.* 2020), while the turions and fragments of *H. verticillata* are drought sensitive (Pickman & Barnes 2017). Because of these characteristics, *H. verticillata* specializes in dispersal through water. The selection of 14 km as the largest threshold distance for dIIC in the structure of path analysis of this study also suggests that *H. verticillata* is well adapted to hydrochory.

Among the group A species, the coverage of *N. japonica*, *N. tetoragon*, and *P. natans* was negatively affected by DTP, which corresponds to the path analysis result of species richness. On the other hand, coverage of *C. demersum* was positively affected by DTP because *C. demersum* can dominate in high phosphorus level waters (Mjelde & Faafeng 1997). *N. tetoragon* and *P. natans* group and *C. demersum* were each positively and negatively affected by TDN in an opposite manner to the effect of DTP, but the reason is unknown. *P. natans* and *C. demersum* were negatively affected by area. Several processes have been suggested in previous studies to encourage the growth of aquatic plants in smaller water bodies (Geest *et al.* 2003). For example, in smaller ponds, aquatic plants (especially submerged plants) have a higher percentage of cover due to the following processes: fish die off and foragers decrease due to lack of oxygen, the water becomes clearer due to an increase in zooplankton using the shoreline as a refuge because of the longer shoreline relative to surface area, and aquatic plants can occupy a body of water for a short period of time once they are established (Geest *et al.* 2003). Further investigation is needed to reveal what processes strongly control the coverage of *P. natans* and *C. demersum*.

The path analysis results for group B suggested that the coverage of *U.* × *japonica* was negatively affected by dIIC and negatively affected by DTP and turbidity in the study area (Fig. 4-2-B). High turbidity can be interpreted as the effect of phytoplankton growth due to eutrophication, where this species fails to establish itself well as a result of low tolerance to eutrophication (Hamashima 2008). Surprisingly, hydrological connectivity had no positive effect on this species in this area. *U.* × *japonica* does not produce seeds because it is a hybrid, but its turions and fragments function as propagules (Kadono 2014). Turions and fragments of this species are intolerant to drying; therefore, *U.* × *japonica* may be dependent on hydrochory for dispersal. Because individuals of these species may die from failure to adapt to the nutrient conditions of the dispersed swamps, the effects of dIIC may not have been detected. Our findings suggest that this species can be dispersed through waterways, but cannot grow due to the effects of eutrophication.

The path analysis results for group C suggested that the coverage of *P. octandrus*, *P. maackianus* and *P. compressus* was unaffected by the dIIC and water quality in the study area (Fig. 4-2-C). All three species of the genus *Potamogeton* are dispersed through seeds and turions (*P. maackianus* does not produce turions but can propagate through fragments). *Potamogeton* seeds have a dry and hard seed coat that resembles grains (Pollux 2011), making them difficult for birds and fish to digest (Smits *et al*. 1989). The seeds pass through the digestive tract, which slightly damages the seed skin and facilitates germination (Santamaria *et al*. 2002; Pollux 2011). Thus, the three species of the genus *Potamogeton* can be dispersed by waterfowl in addition to hydrochory; therefore, it is possible that the effect of dIIC was not detected for these species.

However, the three species of *Potamogeton* in group C were also not significantly affected by nutrient concentrations (DTP and DTN). This is because these three species have high tolerance for eutrophication (Table 2; Kadono 2007).

How should we conserve aquatic plants in floodplain ponds?

The path analysis results for species richness suggested that the species richness of aquatic plants declined as a result of eutrophication, and its effect was greater than that of the hydrological connectivity index. Therefore, the most important conservation measure for the study region is mitigating eutrophication. Identifying sources of nutrient inflow and installing sewage treatment facilities are necessary to control eutrophication in urban areas. Maintaining buffer areas such as wetlands and forests around ponds (Akasaka *et al.* 2010) and removing nutrients from ponds would be effective in controlling nutrient inflow from urban areas. One way to remove nutrients accumulated in ponds is to harvest aquatic plants and reuse them as compost (Tsuda 1972; Ohzono *et al*. 2015). Using aquatic plants as compost aids the removal of excess nutrients released into the hydrosphere. In Lake Biwa, the largest lake in Japan, the traditional compost method is currently used to treat overgrown *H. verticillata* and *P. maackianus* (Hiratsuka et al. 2006; Ohzono *et al.* 2015) and could be applied to aquatic plants such as *Trapa japonica* and *P. compressus* that are overgrown in the study area.

This study also suggests that artificial watercourses between ponds function as dispersal pathways for aquatic plants in lowland floodplains, which suggests that the conservation of hydrologic connectivity is also important for conserving aquatic plants in degraded floodplains. This would be especially important for species that depend on hydrochory (for example, *N. tetragon* and *H. verticillata*). Agricultural ditches may also serve as refuges, depending on the frequency of disturbance and the depth of the water (Rasran & Vogt 2017; Sun *et al.* 2022). On the other hand, connecting channels flowing through nutrient sources may cause nutrient accumulation in floodplain ponds, which may lead to the deterioration of aquatic plant communities in the future. For example, our results imply that *U.* × *japonica* cannot survive in eutrophic ponds despite being dispersed via watercourses. It is important to maintain hydrological connectivity for dispersal; however, such negative influences should also be considered. We believe that taking the above measures for water quality management and connectivity conservation should be the first priority in conserving aquatic plant communities in degraded floodplain ponds.

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Statements and Declarations

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Competing Interests

The authors have no competing financial or non-financial interests to declare.

Author Contribution

All the authors contributed to the conception and design of the study. The survey and analysis designs were developed by Yu Nagata, Nobuo Ishiyama, Futoshi Nakamura, and Junko Morimoto. Yu Nagata performed vegetation surveys, data collection, and analysis. Guidance for the analysis of nutrient level was provided by Hideaki Shibata and Karibu Fukuzawa. The first draft of the manuscript was written by Yu Nagata, and all the authors commented on the previous versions of the manuscript. All authors have read and approved the final manuscript.

Data availability

The datasets generated in the current study are available from the corresponding author upon reasonable request.

Supplementary Table 1. Values of explanatory variables of each pond.

Each column represents a survey pond. Hydrological connectivity is indicated by 1 if the surveyed pond is connected through watercourses to another pond and 0 if it is isolated.

Explanatory Variable	1	2	4	5	6	7	8	11	12	13	14	15	16	17	18	19	20	21	23	24	Average	Standard Deviation
pH (Average)	7.16	6.57	7.15	8.16	6.14	8.49	9.03	6.13	6.96	6.59	6.46	6.39	6.73	6.59	6.07	6.43	5.97	6.60	6.59	6.43	6.83	1
DO (mg/L, Average)	9.19	2.05	7.70	7.60	5.86	7.68	12.38	6.29	7.03	3.58	3.74	2.01	7.88	7.61	5.88	8.26	2.17	0.53	5.28	0.65	5.67	3.12
EC (S/m, Average)	14.33	9.04	24.14	9.62	26.39	15.68	16.46	24.38	14.21	22.04	14.66	10.75	21.81	20.69	14.19	11.13	4.49	29.54	5.10	8.42	15.85	7.18
Turbidity (ONTU, Average)	15.48	55.11	5.51	4.86	6.87	5.89	29.95	3.69	23.57	15.41	9.11	6.39	9.80	22.58	10.44	6.40	4.20	17.05	4.18	14.93	13.57	12.27
Salinity (%, Average)	0.00	0.00	0.10	0.00	0.10	0.00	0.00	0.10	0.00	0.10	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.03	0.05
Depth (cm, Average)	99.67	46.13	108.00	142.93	121.33	100.93	108.67	124.67	88.00	131.00	115.00	77.67	81.00	99.33	97.33	192.67	178.00	102.67	156.21	109.33	114.03	34.13
Depth (cm, Standard Deviation)	26.84	5.30	49.37	68.71	28.74	41.68	31.04	15.92	14.72	23.83	25.43	22.69	12.96	32.05	15.74	43.94	28.94	41.60	8.62	31.18	28.46	15.24
DTN (mg L-1, Average)	0.87	0.45	5.42	9.21	9.21	1.44	3.23	5.46	4.23	2.56	0.55	1.25	0.93	2.20	1.25	0.35	0.46	3.17	0.51	0.84	2.68	2.75
DTP (mg L-1, Average)	0.02	0.03	1.18	0.01	0.01	0.02	0.02	0.02	0.03	0.04	0.08	0.04	0.04	0.02	0.05	0.01	0.01	0.12	0.01	0.07	0.09	0.26
DOC (mg L-1, Average)	10.61	7.57	7.99	6.03	17.67	11.49	12.25	16.41	16.04	15.89	6.08	3.91	9.73	8.18	11.13	6.23	8.88	14.49	6.38	8.43	10.27	4.05
dIIC_0.5km	11.11	0.05	0.27	5.68	0.00	2.20	3.64	1.41	28.52	0.42	0.27	0.77	0.47	0.03	0.43	0.09	0.03	0.08	4.98	0.17	3.03	6.62
dIIC_1km	10.36	0.05	0.25	5.30	0.00	2.05	3.39	7.22	32.48	0.39	0.25	1.27	1.00	0.02	0.69	0.27	0.10	0.07	4.64	0.16	3.50	7.39
dIIC_3km	8.54	0.04	0.21	4.37	0.00	1.69	2.79	8.37	37.91	5.39	2.52	5.27	4.13	1.20	2.88	1.15	0.45	0.06	3.82	0.13	4.55	8.28
dIIC_5km	7.79	0.04	0.19	3.98	0.00	2.02	2.55	8.59	40.31	4.88	3.63	6.58	5.18	1.22	4.54	1.88	0.69	1.51	3.49	0.12	4.96	8.71
dIIC_7.5km	10.21	0.03	0.16	3.31	0.00	6.53	2.12	8.16	37.00	4.48	3.55	6.06	4.75	1.12	4.50	1.80	0.70	1.84	2.89	0.39	4.98	8.05
dIIC_10km	16.80	0.02	0.09	1.92	0.00	8.24	1.23	7.39	35.25	4.26	3.22	5.77	4.53	1.07	4.39	1.75	0.68	1.84	1.68	0.22	5.02	8.15
dIIC_12km	19.14	0.02	0.08	1.72	0.00	8.29	1.10	7.49	34.38	4.26	3.26	5.52	4.41	1.06	4.51	1.80	0.70	1.96	1.51	0.22	5.07	8.19
dIIC_14km	17.98	0.02	0.08	1.60	0.00	9.55	1.02	7.33	35.54	4.30	3.19	5.75	4.56	1.07	4.19	1.67	0.65	1.86	1.40	0.20	5.10	8.35
Farmland ratio (%) _10m	0.04	0.04	0	0	0.04	0.65	0.64	0.91	0.08	0.56	0.05	0	0.74	0.78	0.23	0	0	0.09	0.16	0.96	0.30	0.35
_50m	0.16	0.27	0	0.02	0.26	0.77	0.69	0.92	0.30	0.67	0.12	0.02	0.84	0.86	0.42	0	0	0.10	0.24	0.98	0.38	0.35
_100m	0.49	0.40	0	0.08	0.39	0.85	0.60	0.92	0.54	0.74	0.18	0.10	0.89	0.92	0.64	0.02	0.05	0.12	0.48	0.98	0.47	0.34
_500m	0.82	0.66	0.42	0.34	0.66	0.77	0.79	0.89	0.88	0.93	0.63	0.67	0.88	0.92	0.82	0.40	0.27	0.25	0.86	0.99	0.69	0.23
_1000m	0.85	0.72	0.51	0.55	0.58	0.65	0.62	0.85	0.87	0.87	0.67	0.72	0.83	0.90	0.77	0.51	0.44	0.47	0.84	0.91	0.71	0.16
Urban ratio (%) _10m	0	0	0.41	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0.04	0	0	0.02	0.09
_50m	0	0	0.51	0.07	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0.07	0	0	0.03	0.11
_100m	0	0	0.67	0.14	0	0	0.018	0	0	0.05	0	0	0	0	0	0	0	0.11	0	0	0.05	0.15
_500m	0.02	0	0.34	0.37	0.02	0.02	0.02	0.00	0.01	0.02	0.08	0.02	0	0	0	0.00	0.00	0.17	0	0	0.05	0.11
_1000m	0.01	0.03	0.17	0.17	0.02	0.03	0.05	0.03	0.02	0.02	0.09	0.03	0.01	0.01	0.02	0.11	0.15	0.15	0.02	0.04	0.06	0.06
Farmland+Urban ratio (%)_10m	0.04	0.04	0.41	0.03	0.04	0.65	0.64	0.91	0.08	0.56	0.05	0	0.74	0.78	0.23	0	0	0.13	0.16	0.96	0.32	0.35
_50m	0.16	0.27	0.51	0.09	0.26	0.77	0.69	0.92	0.30	0.67	0.12	0.02	0.84	0.86	0.42	0	0	0.17	0.24	0.98	0.42	0.34
_100m	0.49	0.40	0.67	0.22	0.39	0.85	0.62	0.92	0.54	0.79	0.18	0.10	0.89	0.92	0.64	0.02	0.05	0.24	0.48	0.98	0.52	0.31
_500m	0.84	0.66	0.76	0.71	0.68	0.79	0.80	0.90	0.89	0.94	0.71	0.69	0.88	0.92	0.82	0.40	0.27	0.42	0.86	0.99	0.75	0.19
_1000m	0.86	0.76	0.68	0.72	0.60	0.68	0.67	0.89	0.89	0.89	0.76	0.75	0.84	0.91	0.79	0.62	0.59	0.63	0.87	0.95	0.77	0.12
Area (m^2)	123815.38	6289.53	13755.18	64136.18	1202.48	49232.04	55880.48	29426.57	135768.18	21181.59	18831.56	27720.95	23398.86	4605.77	12938.79	5260.17	2044.28	7371.45	46072.14	7535.70	32823.36	38075.60
Hydrological Connectivity	1	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1		

Supplementary Table 2. Coverage of aquatic plants that appeared at each survey pond.

Each column represents a survey pond. The values in the cells are the average coverage of each aquatic plant in 30 quadrats for each floodplain pond and the Arcsin square conversion. *Lemna* sp. contains *Lemna aoukikusa* Beppu et Murata subsp. *aoukikusa* and *Lemna minor* L.

	1	2	4	5	6	7	8	11	12	13	14	15	16	17	18	19	20	21	23	24
C. demersum	0.14	0.07	0.34	0.01	0.09	0.02	0	0.09	0.10	0.07	0.44	0.11	0.26	0.20	0.20	0.30	0.14	0	0.14	0.18
R. fluians	0.04	0	0	0	0.07	0	0.06	0.02	0.02	0	0	0	0	0.03	0	0.01	0.08	0	0.02	0
Lemna sp.	0.05	0.09	0.49	0.03	0.05	0.03	0	0.09	0.04	0.05	0.17	0.06	0.09	0.06	0.04	0	0.02	0	0.02	0.12
S. polyrhiza	0.05	0.11	0.25	0.03	0.13	0.03	0.02	0.08	0.05	0.01	0.06	0.05	0.06	0.06	0.06	0.03	0.05	0.08	0.03	0.11
U. japonica	0.19	0	0	0.17	0.31	0.25	0	0.12	0.02	0.06	0.04	0.04	0	0.10	0.01	0.34	0.50	0	0.10	0.03
L. trisula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.03	0
H. verticillata	0.14	0	0	0.05	0	0.14	0	0.13	0.11	0.08	0	0	0	0.10	0.06	0.05	0	0	0.06	0.10
N. marina	0.06	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0
P. octandrus	0.04	0.26	0	0.04	0	0.04	0	0.06	0.14	0.04	0.13	0.06	0.10	0.10	0	0	0	0.03	0.07	0
P. maackianus	0.29	0	0	0	0	0	0.06	0	0	0	0	0	0	0.10	0	0.06	0	0	0.03	0
P. campressus	0.09	0	0	0	0.59	0.18	0.06	0.22	0.27	0.12	0.16	0.03	0.17	0.17	0.18	0.10	0.03	0.08	0.36	0.13
M. verticillatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0.15	0	0.29	0.07	0	0.12	0
P. pectinatus	0	0	0	0	0	0	0	0	0.11	0	0	0	0	0	0	0	0	0	0	0
N. minor	0	0	0	0	0	0	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0
P. natans	0	0	0	0.21	0	0	0	0.23	0	0	0	0	0	0.19	0	0	0.19	0	0	0
T. japonica	0.39	0.69	0.20	0.60	0.17	0.30	0.53	0.46	0.55	0.81	0.34	0.83	0.64	0.46	0.71	0.25	0	0.88	0.23	0.57
N. japonica	0.32	0	0	0.20	0	0.37	0.44	0.21	0	0	0.25	0.06	0	0.23	0	0.15	0.25	0	0.46	0.29
N. tetragona	0.07	0	0	0.14	0	0.31	0.07	0.17	0.20	0	0	0	0	0.06	0	0	0	0	0.07	0
B. schreberi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.20	0.29	0	0	0
Number of species	13	5	4	10	7	10	7	12	13	8	8	8	6	14	7	11	10	4	14	8

Supplementary Table 3. Variable selection by round robin combination in path analysis.

We analyzed all combinations of the dIIC threshold distances and physical environments to compare the AIC and RMSEA values between the path analysis. The gray cells indicate the selected model, satisfying RMSEA <0.06 and having the highest fitting degree (i.e., lowest AIC). Regardless of the other explanatory variables, the Urban ratio_100 m (the land use variable) was the highest fitting model.

Species Richness	Physical environment variable									
	Depth		Depth variation		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	194.818	0.085	196.814	0.000	196.086	0.000	196.701	0.058	194.914	0.000
dIIC_1km	195.212	0.082	196.786	0.000	196.476	0.000	196.915	0.000	194.915	0.000
dIIC_3km	192.709	0.073	193.714	0.000	193.685	0.000	194.174	0.000	192.220	0.000
dIIC_5km	192.709	0.073	196.273	0.000	195.937	0.000	196.195	0.000	194.506	0.000
dIIC_7.5km	194.891	0.121	195.869	0.000	195.533	0.000	195.902	0.000	194.077	0.000
dIIC_10km	194.779	0.126	195.875	0.000	195.471	0.000	195.786	0.000	194.019	0.000
dIIC_12km	194.782	0.129	195.876	0.000	195.455	0.000	195.750	0.000	194.005	0.000
dIIC_14km	194.774	0.129	195.902	0.000	195.493	0.000	195.778	0.000	194.044	0.000

Coverage of *N. japonica*	Physical environment variable							
	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	81.137	0.086	83.384	0.000	84.089	0.101	82.113	0.000
dIIC_1km	82.761	0.083	84.744	0.000	84.318	0.049	83.187	0.000
dIIC_3km	84.766	0.079	86.297	0.000	83.509	0.000	84.833	0.000
dIIC_5km	85.289	0.100	86.713	0.000	83.173	0.000	85.283	0.000
dIIC_7.5km	84.798	0.121	86.221	0.000	83.974	0.000	84.761	0.000
dIIC_10km	85.034	0.124	86.476	0.000	83.779	0.000	85.028	0.000
dIIC_12km	85.076	0.126	86.511	0.000	83.779	0.000	85.065	0.000
dIIC_14km	85.082	0.126	86.534	0.000	83.748	0.000	85.089	0.000

Coverage of *N. tetragona*	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	51.962	0.088	52.069	0.000	52.230	0.056	50.325	0.000
dIIC_1km	52.346	0.087	52.941	0.000	52.260	0.000	50.964	0.000
dIIC_3km	56.658	0.091	57.270	0.000	52.196	0.000	55.346	0.000
dIIC_5km	57.185	0.122	57.881	0.000	52.299	0.000	55.977	0.000
dIIC_7.5km	54.664	0.156	55.579	0.000	52.264	0.000	53.653	0.000
dIIC_10km	54.646	0.162	55.513	0.000	52.145	0.000	53.588	0.000
dIIC_12km	54.746	0.165	55.619	0.000	52.141	0.000	53.696	0.000
dIIC_14km	54.520	0.166	55.367	0.000	52.051	0.000	53.443	0.000

Coverage of *H. verticillata*	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	42.399	0.131	42.453	0.000	42.455	0.104	40.456	0.000
dIIC_1km	42.532	0.126	42.457	0.000	42.452	0.000	40.543	0.000
dIIC_3km	42.908	0.103	42.859	0.000	42.302	0.000	40.908	0.000
dIIC_5km	44.160	0.110	44.136	0.000	42.640	0.000	42.164	0.000
dIIC_7.5km	41.964	0.118	41.923	0.000	41.572	0.000	39.977	0.000
dIIC_10km	41.387	0.120	41.339	0.000	41.066	0.000	39.398	0.000
dIIC_12km	41.242	0.122	41.196	0.000	40.927	0.000	39.255	0.000
dIIC_14km	41.185	0.121	41.134	0.000	40.876	0.000	39.194	0.000

Coverage of *U. japonica*	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	64.535	0.198	63.460	0.127	70.747	0.221	71.719	0.227
dIIC_1km	65.283	0.191	63.386	0.112	70.473	0.199	72.738	0.220
dIIC_3km	63.654	0.170	63.011	0.078	72.390	0.176	72.296	0.195
dIIC_5km	63.470	0.161	63.751	0.053	72.401	0.159	72.553	0.170
dIIC_7.5km	64.340	0.164	64.507	0.057	72.313	0.193	73.009	0.166
dIIC_10km	65.685	0.168	65.715	0.065	72.088	0.211	73.625	0.167
dIIC_12km	65.878	0.169	65.954	0.069	72.040	0.215	73.746	0.169
dIIC_14km	65.998	0.169	65.970	0.069	72.040	0.216	73.752	0.168

Coverage of *P. octandrus*	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	40.177	0.099	49.085	0.000	50.887	0.062	52.946	0.000
dIIC_1km	40.236	0.097	49.061	0.000	51.599	0.000	53.132	0.000
dIIC_3km	39.731	0.097	49.010	0.000	53.983	0.000	53.065	0.000
dIIC_5km	39.876	0.118	49.287	0.000	53.811	0.000	53.179	0.000
dIIC_7.5km	40.271	0.131	49.460	0.000	52.973	0.000	53.237	0.000
dIIC_10km	40.367	0.133	49.487	0.000	52.941	0.000	53.235	0.000
dIIC_12km	40.383	0.135	49.496	0.000	52.902	0.000	53.231	0.000
dIIC_14km	40.383	0.134	49.489	0.000	53.010	0.000	53.234	0.000

Coverage of *P. maackianus*	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	55.483	0.091	54.313	0.000	53.377	0.107	53.486	0.000
dIIC_1km	56.023	0.089	54.640	0.000	53.171	0.000	54.037	0.000
dIIC_3km	56.250	0.086	54.993	0.000	54.297	0.000	54.276	0.000
dIIC_5km	56.485	0.109	55.303	0.000	54.266	0.000	54.518	0.000
dIIC_7.5km	56.468	0.126	55.270	0.000	54.221	0.000	54.501	0.000
dIIC_10km	56.148	0.133	54.900	0.019	54.617	0.000	54.184	0.000
dIIC_12km	56.064	0.137	54.807	0.036	54.667	0.000	54.103	0.000
dIIC_14km	56.124	0.136	54.873	0.037	54.645	0.000	54.159	0.000

Coverage of *P. compressus*	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	82.247	0.194	81.841	0.143	81.960	0.144	80.330	0.000
dIIC_1km	81.969	0.196	81.383	0.151	81.845	0.096	80.093	0.000
dIIC_3km	81.605	0.211	81.113	0.169	81.746	0.000	79.790	0.000
dIIC_5km	81.169	0.244	80.738	0.205	81.369	0.000	79.414	0.000
dIIC_7.5km	81.284	0.261	80.841	0.227	81.486	0.079	79.528	0.000
dIIC_10km	81.490	0.264	81.044	0.231	81.709	0.084	79.714	0.000
dIIC_12km	81.520	0.266	81.081	0.233	81.745	0.087	79.746	0.000
dIIC_14km	81.595	0.265	81.149	0.234	81.808	0.085	79.808	0.000

Coverage of *P. natans*	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	58.881	0.132	57.632	0.000	57.142	0.100	57.757	0.000
dIIC_1km	59.116	0.130	57.898	0.000	54.406	0.000	58.032	0.000
dIIC_3km	58.765	0.131	57.671	0.000	52.539	0.000	57.636	0.000
dIIC_5km	58.787	0.150	57.636	0.000	54.530	0.000	57.619	0.000
dIIC_7.5km	58.865	0.164	57.723	0.000	54.728	0.098	57.701	0.000
dIIC_10km	58.881	0.167	57.746	0.000	55.465	0.099	57.729	0.000
dIIC_12km	58.872	0.169	57.733	0.000	55.550	0.102	57.716	0.000
dIIC_14km	58.885	0.169	57.753	0.000	55.702	0.101	57.738	0.000

Coverage of *C. demersum*	Depth		Turbidity		Area		Null	
	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA	AIC	RMSEA
dIIC_0.5km	65.646	0.083	65.890	0.000	68.887	0.102	66.924	0.000
dIIC_1km	65.933	0.080	66.072	0.000	68.829	0.000	67.328	0.000
dIIC_3km	66.259	0.072	66.752	0.000	64.179	0.000	67.525	0.000
dIIC_5km	66.376	0.094	66.841	0.000	68.059	0.000	67.734	0.000
dIIC_7.5km	66.177	0.111	66.658	0.000	68.673	0.000	67.650	0.000
dIIC_10km	66.209	0.115	66.674	0.000	68.710	0.000	67.658	0.000
dIIC_12km	66.208	0.118	66.679	0.000	68.723	0.000	67.661	0.000
dIIC_14km	66.217	0.117	66.674	0.000	68.734	0.000	67.658	0.000

Supplementary Table 4. Explanatory variables (i.e., the dIIC threshold distance and physical environment) and the significant explanatory variables selected by path analysis as the highest fitting model.

‘NA' for selected explanatory variables indicates that there were no path analysis satisfying RMSEA <0.06. ‘Error’ indicates that path analysis could not be constructed. Groupings were selected based on similarities based on the results of the path analysis.

Objective Variables	Selected Explanatory variables		Significant Explanatory variables		Grouping by SEM results
	dIIC	Pysical environment	p<0.05	p<0.01	
Species richness	3km	NA	NA	DTP,dIIC	
Coverage of each species					
N. japonica	0.5 km	NA	DTP, dIIC	NA	A
N. tetragona	0.5 km	NA	DTN, DYP	dIIC	A
H. verticillata	14 km	NA	NA	dIIC	A
U. japonica	5 km	turb	dIIC	DTP, turb	B
P. octandrus	3 km	turb	NA	turb	C
P. maackianus	0.5 km	NA	NA	NA	C
P.compressus	5 km	NA	NA	NA	C
P. natans	3 km	area	DTN	DTP, dIIC, area	A
C. demersum	3 km	area	dIIC, DTN	DTP, area	A
Lemna sp.	NA		-		-
S. polyrhiza	NA		-		-
M. verticillatum	NA		-		-
T. japonica	NA		-		-
B. schreberi	NA		-		-
L. trisulca	Error		-		-
N. minor	Error		-		-
P. pectinatus	Error		-		-
R. fluitans	Error		-		-