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1	Contribution of hydrological connectivity in maintaining aquatic plant communities in remnant floodplain
2	ponds in agricultural landscapes.
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22 <u>Abstract</u>

23	The expansion of the agricultural landscape has led to the fragmentation of floodplains. These remnant
24	floodplain ponds serve as important habitats for aquatic plants. Hydrological connectivity between
25	floodplain ponds, facilitated by artificial watercourses, plays an important role in providing a migration
26	course for mobile animals, such as fish. However, little is known about the contribution of artificial
27	watercourses to the dispersal of aquatic plants, which are passive dispersers, between floodplain ponds.
28	This study aimed to elucidate the effects of hydrological connectivity through artificial watercourses and
29	environmental factors on the structure and composition of aquatic plant communities in lowland floodplain
30	ponds. Vegetation and environmental surveys of 20 floodplain ponds were conducted in the agricultural
31	landscape of northern Japan. Path analysis was used to clarify the effects of local- and landscape-scale
32	environmental variables on aquatic plant communities with respect to species richness and species coverage
33	The path analysis results suggested that both hydrological connectivity between floodplain ponds and
34	eutrophication were influential determinants of the species richness of aquatic plant communities. The study
35	findings indicate that water quality management, connectivity conservation, and restoration should be
36	prioritized to maintain aquatic plant communities in degraded floodplain ponds.
37	

39 Key Words

40 Dispersal; Hydrochory; Artificial Watercourses; Eutrophication.

41

42 Introduction

Wetlands provide habitats for various organisms, such as birds, fishes, and aquatic insects. The total 43 44 global area of wetlands decreased by 35% from 1900 to 2015 (Ramsar 2018), and the total area of wetlands 45 in Japan decreased by 61% from the 1910s to 1999 (Geographical Information Authority of Japan 2000). 46 Such wetland loss causes habitat reduction and fragmentation, leading to a decline in biodiversity by 47 limiting biological dispersal and genetic exchange (Soons et al. 2005; Young et al. 1996). A primary cause 48 of wetland loss in Japan is the conversion of wetlands to farmland and residential land (Geographical 49 Information Authority of Japan 2000). Wetlands face serious loss and degradation, especially in lowland 50 floodplains, owing to their suitability for rice cultivation (Fujita 2017). 51 Aquatic plants found in these habitats include vascular plants, bryophytes, and charophytes, which are 52 adapted to wetland environments and are the primary producers of these wetland ecosystems. Aquatic plants 53 support biodiversity by providing sites for foraging, spawning, and shelter for aquatic organisms and by 54 improving water quality (Kadono 2014). However, aquatic plants are endangered as a result of habitat loss 55 and fragmentation. Approximately 40% of native aquatic plant species in Japan are listed as vulnerable to 56 various environmental changes (Ministry of the Environment Government of Japan 2015).

57	Establishing new habitats and ensuring gene pool interaction through propagule dispersal are essential
58	to conserve aquatic plant communities (Middleton et al. 2006). The propagules of aquatic plants can be
59	dispersed by wind (anemochory), animals (zoochory), and water (hydrochory) (Middleton et al. 2006).
60	Because free-floating, submerged, and floating-leaved plant species inhabit highly water-dependent
61	environments, the propagules of several of these species are adapted to hydrochory and hydrological
62	connectivity promotes their dispersal (Akasaka et al. 2011; Bolpagni et al. 2020; Dahlgren & Ehrlen 2005).
63	Hydrochory also promotes secondary dispersal, allowing propagules to be transported farther (Soomers et
64	al. 2013). Considering these ecological roles, conserving hydrological connectivity is important for the
65	dispersion of aquatic plants.
66	Floodplain ponds are important habitats for aquatic plants because of the high species diversity of aquatic
67	plants compared to other water bodies (e.g., rivers and large lakes) (Geest et al. 2003; Sun et al. 2022). In
68	floodplain ponds, flooding allows dispersal between ponds, and regular disturbances create new habitats
69	(Geest et al. 2003). However, the frequency of flooding has decreased owing to the effects of land use
70	conversion and river channelization, hampering aquatic plant dispersal (Opperman et al. 2010).
71	Hydrological connectivity through artificial watercourses, such as agricultural canals and road drainage
72	canals in lowland areas, plays an important role in providing migration courses for mobile animals, such as
73	fish (Ishiyama et al. 2014, 2015). However, little is known about the contribution of artificial watercourses
74	to the dispersal of aquatic plants between floodplain ponds and the effect of connectivity on the structure

76	The structure and composition of aquatic plant communities are influenced by a variety of factors in their
77	physical environment, such as water depth (Sakurai et al. 2017), water surface area (Geest et al. 2003;
78	Akasaka & Takamura 2012), turbidity (Janne et al. 2013), water temperature (Lacoul & Freedman 2006),
79	water level fluctuations (Lacoul & Freedman 2006), sediment (Ikushima 1972), and water quality
80	parameters, such as pH, electrical conductivity, and nutrient concentration (Takamura et al. 2003; James et
81	al. 2005). In particular, in areas where the land use type has changed, eutrophication progresses faster than
82	it does under natural conditions as a result of nutrient loading caused by human activities in agricultural
83	and urban areas (Lisa & Carolyn 2007). As eutrophication progresses, only plants tolerant to eutrophication
84	survive, resulting in a decrease in aquatic plant diversity (Takamura et al. 2003; James et al. 2005). In
85	addition, phytoplankton blooms lead to an increase in the turbidity of the water column, affecting the light
86	environment and inhibiting the growth of aquatic plants, especially those that are submerged (Matthew et
87	al. 2018).
88	This study aimed to elucidate the effects of hydrological connectivity provided by artificial watercourses,
89	water quality, and physical environments on the structure and composition of aquatic plant communities
90	(that is, species richness and species coverage) in lowland floodplain ponds. In this study, we considered
91	water quality and physical environments in addition to hydrological connectivity for our analyses because
92	knowledge of the relative importance of each factor is essential to develop effective conservation measures.

94 <u>Materials and Methods</u>

95 Study site

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





113 Fig. 1. Map of the study site. The star symbol represents the location of the study region. Agricultural

114 ditches are indicated as open water and represented by a thin straight line.

115



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

121 A vegetation survey was conducted once in each floodplain pond within the period from July to 122 September 2018–2019, when the aquatic plants were thriving. A total of 30 quadrats $(2 \text{ m} \times 2 \text{ m})$ were 123 randomly set on the surface of each floodplain pond and the species names and coverage (in 5% increments) 124 of the aquatic plants that appeared in the quadrats were recorded. Free-floating, submerged, and floating-125 leaved plants, which are frequently dispersed through hydrochory, were targeted during the survey 126 (Dahlgren & Ehrlen 2005). A boat or floater was used to conduct the vegetation surveys. Submerged plants 127 were identified visually if the stems and leaves extended close to the surface of the water. If the plant body 128 was deeply submerged and not clearly visible, the submerged plant was collected by hooking up with a 129 rope and identified. The coverage of deeply submerged vegetation was measured by looking through 130 underwater glasses. Based on the results of the vegetation survey, the total number of aquatic plant species 131 and the average coverage over 30 quadrats were calculated for each aquatic species in each floodplain pond. 132 Species were identified using Kadono (2008, 2014) as reference.

134 Environmental factors

135 Local- and landscape-scale environmental variables were selected to explain the structure and 136 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).

141 The local-scale environmental variables were the physical environment (water depth, water depth 142 variation, area of water surface, and turbidity) and nutrient level (dissolved total nitrogen (DTN) and 143 dissolved total phosphorus (DTP) concentrations). For each quadrat in each floodplain pond, water depth 144 and turbidity were measured using aluminum staff and a multi-item water quality meter (WQC-24, DKK-145 TOA Co., Ltd., Tokyo, Japan), respectively. The average values of these measurements for each floodplain 146 pond were used as local-scale variables. The water depth variation in each floodplain pond was calculated 147 as the standard deviation of the measured water depth. The water surface area of each floodplain pond was 148 calculated using the data available from the National Land Numerical Information (Geographical 149 Information Authority of Japan 2005) using QGIS. To analyze DTN and DTP, surface water was collected 150 at five locations per floodplain pond, and the samples were immediately filtered using glass fiber filter 151 paper (0.7 µm, GF/F, GE Healthcare, Chicago, the United States). The sample filtrate was transferred to the 152 laboratory and stored at -18 °C until further analysis. Subsequently, DTN and DTP in the filtrate were 153 analyzed using a flow-injection analyzer (AACS-4, BL-TEC Inc., Osaka, Japan).

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

159
$$IIC = \frac{\Delta_{l=1} \Delta_{l=1} \Delta_{l=1} A_{L}^{2}}{A_{L}^{2}}$$

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

161 where *i* and *j* represent any floodplain pond combination, a_i represents the area of floodplain pond 162 *i*, A_L represents the total area of all floodplain ponds, and nl_{ij} represents the number of links in the 163 shortest paths between floodplain ponds *i* and *j*.

164

165 The IIC represents the connectivity of floodplain ponds as an entire landscape (all floodplain ponds along 166 the lower Tokachi River). The value of $dIIC_k$ represents the percentage reduction in the IIC that occurs 167 when wetland k is lost (that is, the importance of wetland k in the entire floodplain pond network); 168 floodplain ponds with larger $dIIC_k$ values contribute more toward maintaining the network. The dIIC can 169 be calculated based on the length of the watercourses, assuming that the floodplain ponds are functionally 170 connected. This length is called the threshold distance and can be set on the basis of the territory and 171 dispersal distance of living organisms (Baranyia et al. 2011). However, the dispersal distance of aquatic 172 plants through the watercourses in the study area is unknown. Therefore, based on the studies conducted 173 by Ishiyama et al. (2014, 2015, 2020), the threshold distances were determined to be 0.5, 1, 3, 5, 7.5, 10, 174 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

- 176 was calculated using Conefor 2.6 software (Saura & Torné, April 2012).
- 177 The percentages of farmland, urban, and farmland + urban areas around the floodplain pond were
- 178 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,
- 180 and 1000 m from the pond edge to detect the most influential spatial scale for each of DTN and DTP. Prior
- 181 to that, we used the data obtained by extracting and reclassifying the corresponding land use from 1:25000
- 182 scale vegetation map GIS data (Ministry of Environment 2017). We used QGIS (version 2.18.24) for all
- 183 GIS analyses. The environmental variables were subjected to natural logarithmic transformation to improve
- 184 normality and standardized to make different units comparable.
- 185

186 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.

218 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 <i>et al.</i> 2011; Coetzee <i>et al.</i> 2009; Smits <i>et al.</i> 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 <i>et al.</i> 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 <i>et al.</i> 2017; Geest <i>et al.</i> 2003; Akasaka & Takamura 2012; Janne <i>et al.</i> 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 <i>et al.</i> 2003; James <i>et al.</i> 2005).

220 <u>Results</u>



238	demersum, and Utricularia × japonica) was successfully represented by path analysis (p <0.01)
239	(Supplementary Tables 3 and 4). Out of these nine species, seven unique species were selected and similar
240	analysis results were obtained; based on the results, these species were classified into three groups
241	according to the relative influence of dIIC for discussion: (A) N. japonica, N. tetragona, P. natans, C.
242	demersum and H. verticillata, which were positively influenced by dIIC (Fig. 4-2-A). (B) $U_{\cdot} \times japonica$,
243	which was negatively influenced by dIIC (Fig. 4-2-B). (C) P. octandrus, P. maackianus and P. compressus,

- 244 which were unaffected by dIIC and water quality (Fig. 4-2-C).

246	Table 2. Characteristics of aquatic plants found during the vegetation survey conducted in floodplain ponds.
247	*Ceratophyllum demersum L. includes the possibility of C. platyacanthum Cham. subsp. oryzetorum
248	(Kom.) Les. *'Turion' (in the propagule column) refers to an asexual reproductive organ that is a unique
249	feature of aquatic plants and is formed at the tip or side of the stem. 'Fragments' indicates the ability of the
250	plant to regenerate from fragments. Propagule types mentioned in parentheses occur infrequently. The list
251	is based on the following references: Agami & Waisei (1988), Capers et al. (2010), Coetzee et al. (2009),
252	Hamashima (2008), James et al. (2005), Kadono (1984, 2007, 2008, 2014), Keddy (1976), Matsumoto
253	(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	А
Nymphaea tetragona Georgi var. erythrostigmatica Koji Ito	floating-leaved	VU	perennial	low-mid	seed	А
Brasenia schreberi J.F.Gmel.	floating-leaved	-	perennial	low-mid	seed,turion	-
Potamogeton natans L.	floating-leaved	-	perennial	mid	seed, turion	А
Trapa japonica Flerow	floating-leaved	-	annual	high	seed	-
Utricularia × japonica Makino	free-floating	NT	perennial	low-mid	trion, fragments	В
<i>Lemna aoukikusa</i> Beppu et Murata subsp. <i>aoukikusa</i>	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	А
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	С
Potamogeton maackianus A.Benn.	submerged	-	perennial	high	seed, fragments	С
Potamogeton compressus L.	submerged	-	perennial	high	seed, turion	С
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	-

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

263	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.



265

Result of path analysis where the objective variable is coverage ratio for each aquatic plant species.
 2-A) Species positively affected by dIIC.



2-B) Species negatively affected by dIIC.



267

268 Fig. 4 Results of the path analysis depicting the direct and indirect effects of hydrological connectivity, land

269 use, and local habitat quality on the species richness and coverage of endangered aquatic plants. The

270 numbers indicate the standardized path coefficients estimated using the maximum likelihood method. Thick

- 271 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,

273 respectively.

274 <u>Discussion</u>

275 Effect of hydrological connectivity and local environments on species richness

276 We found that hydrological connectivity between floodplain ponds was suggested to be a significant 277 determinant of the species richness of aquatic plant communities. The path analysis results that the species 278 richness increased with increasing dIIC_3 km in the study area (Fig 4-1). This indicates that watercourse 279 connectivity increases the chances of propagule supply (Akasaka et al. 2012). Even at low velocity, wind 280 can move propagules over the water surface (Soomers et al. 2013), and heavy rainfall can temporally 281 promote dispersal. Therefore, we believe that hydrological connectivity through watercourses increases the 282 likelihood of dispersal for aquatic plants. As emphasized in this study and in previous studies (Akasaka et 283 al. 2012; Bolpagni et al. 2020; Ishiyama et al. 2014, 2015; Soomers et al. 2013), watercourses in lowland 284 floodplains can be important dispersal pathways for aquatic plants. The path analysis selected 3 km as the 285 threshold distance for the dIIC, which implies that 3 km can be regarded as the comprehensive dispersal 286 distance encompassing all aquatic plants in the study region. 287 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
- 290 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

292	in the number of aquatic plant species that can survive in these ponds (Jeppesen et al. 2000). It has also
293	been shown that land use (especially urban) at a 100 m scale more strongly affects water quality than that
294	at larger landscape scales in summer when dissolved nutrients are concentrated by evaporation of pond
295	water (Kuranchie et al. 2022; Zhang et al. 2019). The sewerage penetration rate (number of households
296	equipped with sewerage systems among the total households in the town) in the study area was 86.0% in
297	Toyokoro Town and 72.2% in Ikeda Town as of 2019 (Ikeda Town Hall 2021, Toyokoro Town Hall 2022).
298	The specific source of nutrient runoff in the urban area in this study site is not well understood; however,
299	identifying the source and taking appropriate measures is necessary to prevent eutrophication of floodplain
300	ponds. In contrast to DTP, DTN did not affect species richness. In the study region, more than half of the
301	surveyed ponds exceeded the baseline for eutrophication, that is, over 1 mg L ⁻¹ of TN, which is defined as
302	the minimum level that is not considered unpleasant in the daily lives of citizens (Level 5) (Ministry of the
303	Environment Government of Japan 2019). Even in the study sites, where the extent of eutrophication was
304	below Level 5, the variation in DTN was small. However, there was a large variation in DTP below Level
305	5 (TP of 0.1 mg L^{-1}) among the study sites. This indicates that phosphorus, rather than nitrogen, may be a
306	major factor regulating eutrophication in this area (Jeppesen et al. 2000). However, this result is derived
307	from the assumption that the hypothetical paths encompass the conditions necessary for the establishment
308	of aquatic plants in this region, and further studies are needed to elucidate other cause-and-effect
309	relationships among the environmental variables that we could not consider in this study.

311 Effects of hydrological connectivity and local environments on each species 312 The path analysis results for group A suggested that the coverage of N. japonica and N. tetragona was 313 positively affected by dIIC 0.5 km, that of P. natans and C. demersum was positively affected by dIIC 3 314 km, and that of *H. verticillata* was positively affected by dIIC_14 km in the study area (Fig. 4-2-A). N. 315 japonica and N. tetragon reproduced exclusively through seeds. These species might be unsuitable for 316 zoochory because the seeds of related species (Nuphar lutea and Nymphaea alba) are easily digested by 317 birds and fish and are vulnerable to drying (Smits et al. 1989). A minimum scale of 0.5 km was selected as 318 the dIIC threshold distance, thus confirming that N. japonica and N. tetragon have poor dispersal ability 319 and depend on hydrochory (Smits et al. 1989). 320 Hydrological connectivity between habitats may aid in the dispersal of hydrochory-specific species, as 321 previously emphasized (Akasaka et al. 2012; Bolpagni et al. 2020; Ishiyama et al. 2014, 2015; Soomers et 322 al. 2013). Among Group A species, H. verticillate, P. natans and C. demersum can be easily propagated 323 through turions and fragments. These characteristics make H. verticillata an invasive alien species in North 324 America and C. demersum in New Zealand (Umetsu et al. 2012; Global Invasive Species Database 2022). 325 Of the three species, H. verticillata has a high ability to regenerate from fragments (Umetsu et al. 2012) 326 and has expanded its distribution by attaching fragments to recreational boats and moving in running water 327 (Coetzee et al. 2009). In addition, turions and fragments of related species of P. natans (Potamogeton

329	2013; Heidbuchel et al. 2020), while the turions and fragments of H. verticillata are drought sensitive
330	(Pickman & Barnes 2017). Because of these characteristics, <i>H. verticillata</i> specializes in dispersal through
331	water. The selection of 14 km as the largest threshold distance for dIIC in the structure of path analysis of
332	this study also suggests that <i>H. verticillata</i> is well adapted to hydrochory.
333	Among the group A species, the coverage of N. japonica, N. tetoragon, and P. natans was negatively
334	affected by DTP, which corresponds to the path analysis result of species richness. On the other hand,
335	coverage of C. demersum was positively affected by DTP because C. demersum can dominate in high
336	phosphorus level waters (Mjelde & Faafeng 1997). N. tetoragon and P. natans group and C. demersum
337	were each positively and negatively affected by TDN in an opposite manner to the effect of DTP, but the
338	reason is unknown. P. natans and C. demersum were negatively affected by area. Several processes have
339	been suggested in previous studies to encourage the growth of aquatic plants in smaller water bodies (Geest
340	et al. 2003). For example, in smaller ponds, aquatic plants (especially submerged plants) have a higher
341	percentage of cover due to the following processes: fish die off and foragers decrease due to lack of oxygen,
342	the water becomes clearer due to an increase in zooplankton using the shoreline as a refuge because of the
343	longer shoreline relative to surface area, and aquatic plants can occupy a body of water for a short period
344	of time once they are established (Geest et al. 2003). Further investigation is needed to reveal what
345	processes strongly control the coverage of <i>P. natans</i> and <i>C. demersum</i> .

crispus and Potamogeton richardsonii) and C. demersum are drought tolerant to some extent (Barnes et al.

346	The path analysis results for group B suggested that the coverage of $U_{\cdot} \times japonica$ was negatively
347	affected by dIIC and negatively affected by DTP and turbidity in the study area (Fig. 4-2-B). High turbidity
348	can be interpreted as the effect of phytoplankton growth due to eutrophication, where this species fails to
349	establish itself well as a result of low tolerance to eutrophication (Hamashima 2008). Surprisingly,
350	hydrological connectivity had no positive effect on this species in this area. $U \times japonica$ does not produce
351	seeds because it is a hybrid, but its turions and fragments function as propagules (Kadono 2014). Turions
352	and fragments of this species are intolerant to drying; therefore, $U_{\cdot} \times japonica$ may be dependent on
353	hydrochory for dispersal. Because individuals of these species may die from failure to adapt to the nutrient
354	conditions of the dispersed swamps, the effects of dIIC may not have been detected. Our findings suggest
355	that this species can be dispersed through waterways, but cannot grow due to the effects of eutrophication.
356	The path analysis results for group C suggested that the coverage of <i>P. octandrus</i> , <i>P. maackianus</i> and <i>P.</i>
357	compressus was unaffected by the dIIC and water quality in the study area (Fig. 4-2-C). All three species
358	of the genus Potamogeton are dispersed through seeds and turions (P. maackianus does not produce turions
359	but can propagate through fragments). Potamogeton seeds have a dry and hard seed coat that resembles
360	grains (Pollux 2011), making them difficult for birds and fish to digest (Smits et al. 1989). The seeds pass
361	through the digestive tract, which slightly damages the seed skin and facilitates germination (Santamaria et
362	al. 2002; Pollux 2011). Thus, the three species of the genus Potamogeton can be dispersed by waterfowl in
363	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).

367

368 How should we conserve aquatic plants in floodplain ponds?

369 The path analysis results for species richness suggested that the species richness of aquatic plants 370 declined as a result of eutrophication, and its effect was greater than that of the hydrological connectivity 371 index. Therefore, the most important conservation measure for the study region is mitigating eutrophication. 372 Identifying sources of nutrient inflow and installing sewage treatment facilities are necessary to control 373 eutrophication in urban areas. Maintaining buffer areas such as wetlands and forests around ponds (Akasaka 374 et al. 2010) and removing nutrients from ponds would be effective in controlling nutrient inflow from urban 375 areas. One way to remove nutrients accumulated in ponds is to harvest aquatic plants and reuse them as 376 compost (Tsuda 1972; Ohzono et al. 2015). Using aquatic plants as compost aids the removal of excess 377 nutrients released into the hydrosphere. In Lake Biwa, the largest lake in Japan, the traditional compost 378 method is currently used to treat overgrown H. verticillata and P. maackianus (Hiratsuka et al. 2006; 379 Ohzono et al. 2015) and could be applied to aquatic plants such as Trapa japonica and P. compressus that 380 are overgrown in the study area.

381 This study also suggests that artificial watercourses between ponds function as dispersal pathways for

382	aquatic plants in lowland floodplains, which suggests that the conservation of hydrologic connectivity is
383	also important for conserving aquatic plants in degraded floodplains. This would be especially important
384	for species that depend on hydrochory (for example, N. tetragon and H. verticillata). Agricultural ditches
385	may also serve as refuges, depending on the frequency of disturbance and the depth of the water (Rasran &
386	Vogt 2017; Sun et al. 2022). On the other hand, connecting channels flowing through nutrient sources may
387	cause nutrient accumulation in floodplain ponds, which may lead to the deterioration of aquatic plant
388	communities in the future. For example, our results imply that $U_{\cdot} \times japonica$ cannot survive in eutrophic
389	ponds despite being dispersed via watercourses. It is important to maintain hydrological connectivity for
390	dispersal; however, such negative influences should also be considered. We believe that taking the above
391	measures for water quality management and connectivity conservation should be the first priority in
392	conserving aquatic plant communities in degraded floodplain ponds.
393	
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- 586
- 587 <u>Statements and Declarations</u>
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- 592 *Competing Interests*
- 593 The authors have no competing financial or non-financial interests to declare.
- 594 Author Contribution
- 595 All the authors contributed to the conception and design of the study. The survey and analysis designs
- 596 were developed by Yu Nagata, Nobuo Ishiyama, Futoshi Nakamura, and Junko Morimoto. Yu Nagata

- 597 performed vegetation surveys, data collection, and analysis. Guidance for the analysis of nutrient level
- 598 was provided by Hideaki Shibata and Karibu Fukuzawa. The first draft of the manuscript was written
- 599 by Yu Nagata, and all the authors commented on the previous versions of the manuscript. All authors
- 600 have read and approved the final manuscript.
- 601 Data availability
- 602 The datasets generated in the current study are available from the corresponding author upon
- 603 reasonable request.

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

606 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		i i

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

609 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

610 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

613 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.

	Physical environment variable										
Species	Depth		Depth variation		Turbi	dity	Are	ea	Null		
Richness	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	

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	Physical environment variable													
Coverage of	De	oth	Turb	idity	Ar	ea	Null							
м. јаропіса	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	De	pth	Turb	idity	Ar	ea	Null		
N. tetragona	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	De	oth	Turb	idity	Ar	ea	Null		
H. verticillata	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	Depth		Turbidity		Area		Null	
U. japonica	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	Depth		Turbidity		Area		Null	
P. octandrus	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	Depth		Turbidity		Area		Null	
P. maackianus	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	Depth		Turbidity		Area		Null	
P. compressus	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	Depth		Turbidity		Area		Null	
P. natans	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	Depth		Turbidity		Area		Null	
C. demersum	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

631	Supplementary Table 4. Explanatory variables (i.e., the dIIC threshold distance and physical
632	environment) and the significant explanatory variables selected by path analysis as the highest fitting
633	model.
634	'NA' for selected explanatory variables indicates that there were no path analysis satisfying RMSEA
635	<0.06. 'Error' indicates that path analysis could not be constructed. Groupings were selected based on
636	similarities based on the results of the path analysis.

Obiestive Merichles	Selected	d Explanatory variables	Significant Ex	Grouping by	
Objective variables	dIIC	Pysical environment	p<0.05	p<0.01	SEM results
Species richness	3km	NA	NA	DTP,dIIC	
Coverage of each species					
N. japonica	0.5 km	NA	DTP, dIIC	NA	А
N. tetragona	0.5 km	NA	DTN, DYP	dIIC	А
H. verticillata	14 km	NA	NA	dIIC	А
U. japonica	5 km	turb	dIIC	DTP, turb	В
P. octandrus	3 km	turb	NA	turb	С
P. maackianus	0.5 km	NA	NA	NA	С
P.compressus	5 km	NA	NA	NA	С
P. natans	3 km	area	DTN	DTP, dIIC, area	А
C. demersum	3 km	area	dIIC, DTN	DTP, area	А
<i>Lemna</i> 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		-	-