

Trait-based evaluation of plant assemblages in traditional farm ponds in Korea: Ecological and management implications

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ABSTRACT

The Korean traditional farm pond called *dumbeong* is an important rural landscape element that supports local biodiversity and is useful in irrigating agricultural fields during dry periods. This study assesses how plant communities in *dumbeongs* respond to adjacent land use, water depth, open-water surface, and nutrient levels and irrigation usage. Plant functional and species groups, based on trait and species data respectively from 20 *dumbeongs* in Seocheon-gun, South Korea, were classified by hierarchical analysis and non-metric multidimensional scaling. Relationships between the plant community composition and explanatory variables at both the species and functional group levels were tested through redundancy analysis. The results showed that irrigation usage prevented nutrient accumulation and water depth reduction of the ponds, and we found water depth was the only significant factor that determined plant composition at both species and functional group levels. The plant functional groups were more useful than plant species in predicting plant composition in *dumbeongs*, owing to their collective response to water depth and open-water surface. Our results demonstrate that management practices of *dumbeong*, such as periodic drainage, sediment removal and control of dominant plant species, alter its plant communities and thus need to be considered for biodiversity conservation in agricultural landscapes.

INTRODUCTION

Wetland ecosystems provide important ecological services by capturing nutrients and supporting biodiversity (Hansson *et al.*, 2005). Agroecological land uses that embrace wetlands can help to prevent rural biodiversity loss associated with agricultural intensification (Benton *et al.*, 2003; Michel *et al.*, 2007). Farm ponds, despite their small size and isolation, are important in supporting biodiversity in agricultural landscapes (Williams *et al.*, 2004; Oertli *et al.*, 2005; Casas *et al.*, 2012), and quantitative and theoretical

studies have discussed the ecological values of ponds as habitats in terms of biological diversity (Downing and Leibold, 2002; Downing, 2005; Gioria *et al.*, 2010; Santi *et al.*, 2010; Landi *et al.*, 2012; Zhang *et al.*, 2015).

The Korean traditional farm pond *dumbeong*, meaning “a puddle,” is particularly useful in dry periods as a secondary water source for rice paddy fields. It is constructed by digging a small pit (< 500 m²) in the marginal areas of agricultural fields where water collects (Tab. S1). A *dumbeong* enhances farm biodiversity by providing habitat for various organisms (Kim *et al.*, 2011; Choe *et al.*, 2013, 2016). However, with the adoption of mechanized irrigation and agricultural intensification practices, *dumbeongs* are coming into disuse (Huang *et al.*, 2012).

Dumbeongs are situated in landscapes that are impacted by the anthropogenic forces of habitat degradation, water pollution, and hydroperiod alteration which are factors that affect plant communities in ponds (Wood *et al.*, 2003; Edvardsen and Økland, 2006; Deegan *et al.*, 2007). Land use in adjacent areas has been studied to be significantly associated with the deterioration of water quality in ponds, affecting plant species diversity (Søndergaard *et al.*, 2005; Declerck *et al.*, 2006; Akasaka *et al.* 2010; Alahuhta and Aroviita, 2016). Periodic pond drainage and low fish density have been seen to facilitate diverse plant taxa (Lemmens *et al.*, 2013), and sediment removal coupled with periodic drainage can be a strategy to mitigate the loss of wetland plant species of high

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Key words: Pond ecology; irrigation; plant composition; plant functional group; trait; biodiversity.

Edited by: Rossano Bolpagni, University of Parma, Italy.

Received: 30 September 2018.

Accepted: 28 December 2018.

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J. Limnol., 2019; 78(1): 92-106
DOI: 10.4081/jlimnol.2019.1861

conservation value (Sayer *et al.*, 2012). Numerous studies have discussed the effects of anthropogenic disturbances on ponds, nonetheless the relationship between anthropogenic activities and plant composition of farm ponds remains unclear, as the interacting environmental variables are complex (Gallego *et al.*, 2014; Hassall and Anderson, 2015). Some studies have concluded that the variation in the composition of pond plant communities is due to stochastic events including both natural and anthropogenic factors (Del Pozo *et al.*, 2010; Sayer *et al.*, 2012; Hassall and Anderson, 2015).

Focusing on traits measured at the individual level instead of plant species can help to reduce uncertainty in the multi-layered analysis of biodiversity in ponds (McGill *et al.*, 2006). The study of functional traits is a method to distinguish between selective and random processes by detecting co-occurring species in the functional trait space when a community responds to disturbances (Villéger *et al.*, 2011; Mouillot *et al.*, 2013). A functional group can be composed of species with similar traits that reveal an assembly rule (Keddy *et al.*, 1992). This integration of species and trait data can be useful to identify specific groups of plant species along with the environmental gradient in ponds.

The studies of the composition of plant communities in *dumbeongs* on the basis of functional traits can help to understand biodiversity and ecosystem functions, and inform conservation decisions for *dumbeongs*. In doing so, functional groups may provide focused insights for the patterns of plant communities in *dumbeongs*, whose environments are affected by management practices. Hence, our study has three objectives: i) identify appropriate functional groups of plant species in selected *dumbeongs* to predict plant composition using explanatory variables, ii) compare the explained variation of species-based composition to that of functional group-based composition, and iii) understand the relationship between management and plant compositions.

METHODS

We investigated 20 *dumbeongs* in Seocheon, South Korea, located in the downstream area of Geumgang Basin (Fig. 1). The area of Seocheon is about 400 km², of which 40% is covered with forest and 29% with rice paddy fields (National Geographic Information Institute, 2014). The annual mean temperature and precipitation are 12.3°C and 1349.2 mm, respectively (Seocheon County, 2016). Many *dumbeongs* in Seocheon have been destroyed due to the introduction of mechanized irrigation and the expansion of arable lands. Most of the remaining *dumbeongs* are permanent ponds located in or near valleys, which hinders their conversion to other land uses. The investigated *dumbeongs* in Seocheon share three key

characteristics: they were originally constructed to provide water to crop fields and have been managed by private owners, and they are < 500 m² in area (Tab. S1). As rice paddy fields have gradually been abandoned and irrigation methods have changed, only 13 of the 20 *dumbeongs* investigated are still used for irrigation. The others are used as fish ponds or have been abandoned.

The percentage of plant cover was visually estimated by two experts through a complete survey. Whole plants covering the water surface and an area including a 10 cm buffer boundary of land from the shore line of the *dumbeong* were sampled. The buffer boundary was set to understand the influence of water regime on plant cover of bank. It is noted that the water level of *dumbeongs* had not significantly changed due to no rain since it was fully restored in spring. The *dumbeongs* were not divided into quadrats because the plants were primarily distributed in relatively small areas. The plant cover data were assigned to six classes of the mid-point cover (*i.e.*, <1% estimated as 0.5%, <5% as 3%, <25% as 14%, <50% as 37.5%, <75% as 62.5%, and >75% as 87.5%) to reduce bias in the subjective estimation. The plant data were collected in August 2016 - the peak period of plant cover for the year.

Three types of land use data, including agricultural land (Agri), forest (Forest), and freshwater (Water), were extracted from a digitized map (National Geographic Information Institute, 2014), using the ArcGIS version 10.1 (ESRI, Redlands, CA, USA). The proportion of 3 land use types for areas within a radius of 100 or 200 m from the *dumbeong* edges was calculated to extract six land use variables (Agri100, Agri200, Water100, Water200, Forest100, and Forest200), the extents of which were set to avoid spatial autocorrelation among the *dumbeongs*. Land covers of human settlement and road were not evaluated as those were a little varied and far from *dumbeongs*. Studies have reported that adjacent land uses in those ranges influenced vegetation structure and water properties in farm ponds (Declerck *et al.*, 2006; Akasaka *et al.*, 2010). The boundaries of *dumbeongs* were set as waypoints and were tracked by using a global positioning system (GPS) device (Garmin 60CSx, Olathe, KS, USA), and the surface area was calculated using GIS software (QGIS 2.10.1 Pisa). The mean depth was calculated from the measurements obtained at 1 and 2 m from the land-water interface every 2 m along the long axes of the ponds using a meter stick. We chose these sampling points because all types of mesohabitats (defined by different types of dominant vegetation and areas of open-water surface) were included in this range.

The area of open-water was recorded as percent of the total *dumbeong* area, and defined as the surface area without vegetation, except for the coverage by woody plants above 1 m from the water surface and by submerged plants. As the area of open-water was also

visually estimated by two observers, it was transformed into the mid-point cover following an approach similar to that of the plant data. Water samples were obtained on the same date as the vegetation survey in August 2016. The electric conductivity (EC) was measured *in situ* by specific conductance using handheld probes (Model 30; YSI, Yellow Springs, OH, USA). The water samples were collected by submerging a clean plastic bottle in the open-water to a depth of 20 cm. When the depth was less than 20 cm, the surface water was collected carefully to avoid the inclusion of substratum materials. We measured pH with an automatic titration device (877 Titrino Plus; Metrohm, Herisau, Switzerland) in laboratory before the water samples were filtered using a 250-mL vacuum filter/storage bottle with a 0.45- μ m cellulose acetate membrane (Corning Inc., Corning, NY, USA). The concentration of major cations and nutrient ions was determined in the laboratory by ion chromatography (ICS-1600; Dionex, Sunnyvale, CA, USA). The concentration of dissolved organic carbon (DOC) and

total dissolved nitrogen (TN) was measured using a Shimadzu analyzer (TOC-VCPH with unit TNM-1; Shimadzu Co., Kyoto, Japan).

We collected data on irrigation usage through interviews with pond owners in July and August 2016. As the aim of this study was to determine the influence of management practices on plant compositions in the *dumbeongs*, based on the interviews and findings of previous studies we categorized the *dumbeongs* into two types according to their irrigation usage: *dumbeongs* where the sediment was removed regularly for the past five years (irrigation, IR), and *dumbeongs* that were not maintained in this way (non-irrigation, NIR). A five-year period was considered as it is the minimum required for ecosystem development for the newly constructed ponds to perform a steady ecosystem function (Mitsch and Wilson, 1996). Planting, removal of vegetation, usage of biocides, and fish breeding were also documented by interviewing the owners and conducting field surveys.

Seven types of plant traits were selected in the light

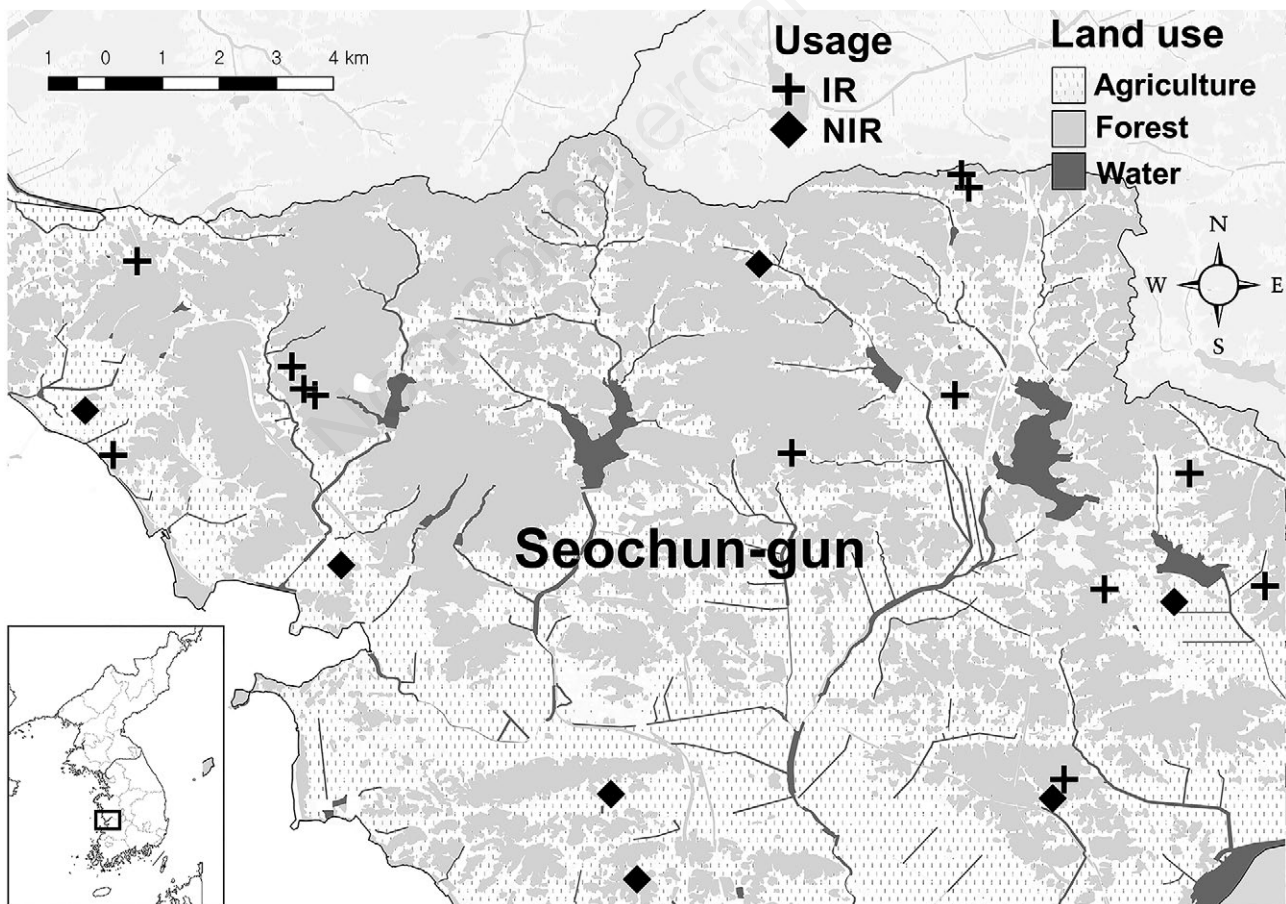


Fig. 1. Locations of the 20 *dumbeong* study sites in Seochun, Korea. IR, ponds used for irrigation regularly in recent 5 years; NIR, ponds not used for irrigation for more than 5 years.

of literature review and advice of wetland experts (Tab. 1). The trait data were collected from online databases (Kühn *et al.*, 2004; Kleyer *et al.*, 2008; Kattge *et al.*, 2011; Laboratory of Wild Plant Science, 2014; USDA/NRCS, 2014; eFloras, 2016; Korea National Arboretum, 2016), literature searches (Morishima and Oka, 1976; Van *et al.*, 1976; Raven, 1992; Gichuki *et al.*, 2001; Katori *et al.*, 2002; Choung *et al.*, 2012; Cho *et al.*, 2013), and field surveys. Hierarchical cluster analysis was used to classify 37 plant species found in the *dumbeongs* into functional groups by generating a dendrogram. The Ward method and squared Euclidean distance were selected from the options available in SPSS ver. 20.0 (IBM, Armonk, NY, USA). The cutting point of the dendrogram was chosen to include at least three species characterized by particular traits in each functional group.

As all trait data were binary, parametric methods such as ANOVA were not used to detect the traits that can separate species into distinct functional groups. Instead, significant differences in trait composition among the functional groups were calculated using the analysis of similarities (ANOSIM). Differences among the functional groups were described and visualized by computing the non-metric multidimensional scaling (NMDS) ordination with fitted vectors of traits from species-trait data matrix using the *metaMDS* and *envfit* functions of the *vegan* package in the R statistics software (Oksanen *et al.*, 2016).

The statistical analyses were performed using

standardized variables (Z-score), and the plant community data were log-transformed to reduce inequality of variances. The correlation between explanatory variables was tested by Spearman rank correlation test. Mann-Whitney *U*-test was performed to test the differences in environmental and land use variables between the management types. The principal component analysis (PCA) was used to explore the patterns of water chemistry and adjacent land use variables among the *dumbeongs*. The PCA reduces the number of correlated variables, thus avoids the multicollinearity problem.

The redundancy analysis (RDA) was performed to reveal the effect of explanatory variables on the composition of plant communities of the *dumbeong*. The RDA is a constrained ordination method that tests the linearized relationship between a set of response and predictor variables (Legendre and Legendre, 2012). The RDA was used to evaluate the effects of environmental and spatial variables on the species and functional group composition, respectively. The RDA results provide visualized propensities of individual species or functional groups for specific predictors. The RDA model is constructed using the stepwise both-selection method. Statistical significance was tested using a randomized permutation test. All statistical analyses were performed using the R statistics software (R Development Core Team, 2016) and SPSS ver. 20.0 (SPSS Inc, Chicago, IL, USA).

Tab. 1. Summary of the selected plant traits.

Trait	Category	Description
Life history	Annual	Lifespan: 1 year
	Perennial	Lifespan: > 2 years
Aquatic plants morphology	Emergent	Leaves and stems pierce the water surface
	Floating-leaf	Floating leaves and rooting to ground
	Floating	Floating leaves and rooting in water
	Submerged	Growing entirely underwater
Vegetative propagation	Below	Propagate by below ground (<i>e.g.</i> , rhizome)
	Above	Propagate by above ground (<i>e.g.</i> , stolon, frond fragmentation)
Wetland indicator status	OBL	Wetland occurrence: >99%
	FACW	Wetland occurrence: 67% ~ 99%
	FAC	Wetland occurrence: 34% ~ 67%
	FACU	Wetland occurrence: 34% ~ 1%
	UPL	Wetland occurrence: <1%
Seed morphology	Balloon	Balloon like appendage, structures for keeping air around seeds
	Elongated	Hook or feather like appendage
	No appendage	None of above
Photosynthesis pathways	C3	C ₃ fixation plants
	C4	C ₄ fixation plants
Growth form	Woody	Trees, shrubs
	Graminoid	True grasses and grass like plants

OBL, obligate wetland; *FACW*, facultative wetland; *FAC*, facultative; *FACU*, facultative upland; *UPL*, obligate upland.

RESULTS

Adjacent land use and local environment of the *dumbeongs*

Among the three physical descriptors of the ponds, the area of open-water and water depth were significantly different between the IR and NIR *dumbeongs* (Tab. 2). The first two principal component axes of the spatial variables explained 70% of the variation among the *dumbeongs* (Tab. 3). The first axis LU1 showed negative and positive correlations with the agricultural and forested areas, respectively. According to the variation along LU1, most of the IR and NIR *dumbeongs* were separated into two groups - adjacent agricultural and forested areas, respectively (Tab. 3, Fig. 2a). The second axis LU2 showed the patterns of adjacent water bodies; however, there was no distinct trend for the management types (Fig. 2a).

The first principal component axis of the water chemical variables, Chem1 which explained 49% of the total variation, showed positive intercorrelations between

the EC and concentrations of major cations and nitrogen nutrients (Tab. 3). The DOC and pH created two independent axes that explained 23% and 12% of the variation, respectively. According to the water chemistry PCA ordination, the concentration of water nutrients and EC were relatively high in the NIR *dumbeongs* (Fig. 2b). However, only two water chemistry variables, EC and sodium ion concentration, were significantly higher in the NIR *dumbeongs* than in the IR *dumbeongs* (Tab. 2). Furthermore, the correlations among the PCA axes extracted from land use and water chemistry variables were not significant (Fig. S1, Fig. S2).

Plant functional groups

The dendrogram shows six plant functional groups classified by the cluster analysis (Fig. 3) and ANOSIM confirmed significant differences among the plant functional groups (R static = 0.87, P = 0.001). The plant functional groups (FG1, FG2, FG3, FG4, FG5, and FG6) were mainly defined by four categories of traits - wetland indicator status, life history, vegetative propagation, and

Tab. 2. Land use and local environment variables (mean± standard error) of the *dumbeongs*. The land use variables are percentage of cover of agricultural (Agri100, Agri200), forested (Forest100, Forest2000) and water areas (Water100, Water200) within 100 and 200 m from edges of the *dumbeongs*, respectively.

Variables	IR	NIR	P
Land uses			
Agri100 (%)	17.9±2.4	30.1±1.8	**
Agri200 (%)	28.6±2.9	52.3±6.6	*
Forest100 (%)	59.0±6.7	30.7±8.8	*
Forest200 (%)	46.2±4.5	42.8±11.0	ns
Water100 (%)	0.4±0.4	0.4±0.3	ns
Water200 (%)	2.5±0.7	1.2±0.8	ns
Local environment			
Area (m ²)	175±39	222±46	ns
Depth (cm)	82±9	31±8	**
Open (%)	47±11	4±1	*
Conductivity (μS·cm ⁻¹)	148±17	216±25	*
pH	7.0±0.1	6.9±0.1	ns
Na ⁺ (mg·L ⁻¹)	9.93±1.09	16.11±1.50	**
K ⁺ (mg·L ⁻¹)	2.81±0.79	5.07±1.70	ns
Mg ²⁺ (mg·L ⁻¹)	3.97±0.56	5.29±0.79	ns
Ca ²⁺ (mg·L ⁻¹)	10.75±2.14	16.00±1.94	ns
TN (mg·L ⁻¹)	0.75±0.22	1.20±0.41	ns
NO ₂ ⁻ (mg·L ⁻¹)	0.02±0.02	0.10±0.05	ns
NO ₃ ⁻ (mg·L ⁻¹)	0.45±0.23	0.80±0.40	ns
DOC (mg·L ⁻¹)	5.66±0.80	4.89±0.67	ns

IR, ponds used for irrigation regularly in recent 5 years; NIR, ponds not used for irrigation for more than 5 years; TN, total dissolved nitrogen; DOC, total dissolved organic carbon; Open, the percentage area of open-water surface. Significant differences were tested by Mann-Whitney U-test: *P<0.05, **P<0.01, nsP>0.05.

Tab. 3. Principal component analysis (PCA) results of the land use and water chemistry variables. The land use variables are percentage of cover of agricultural (Agri100, Agri200), forested (Forest100, Forest2000) and water areas (Water100, Water200) within 100 and 200 m from edges of the *dumbeongs*, respectively.

PCA Axes			
Land use variables	LU1	LU2	
Agri100	-0.57	0.04	
Agri200	-0.50	-0.05	
Forest100	0.56	0.08	
Forest200	0.27	0.48	
Water100	0.21	-0.54	
Water200	0.02	-0.68	
Water chemical variables	Chem1	Chem2	Chem3
Conductivity	0.41	-0.19	0.12
Mg ²⁺	0.39	-0.22	-0.10
Ca ²⁺	0.36	-0.21	-0.02
Na ⁺	0.35	-0.14	0.24
K ⁺	0.21	-0.47	-0.15
TN	0.35	0.26	-0.28
NO ₂ ⁻	0.34	0.29	-0.22
NO ₃ ⁻	0.31	0.40	-0.16
DOC	0.03	-0.56	-0.32
pH	0.12	-0.04	0.80

TN, total dissolved nitrogen; DOC, total dissolved organic carbon.

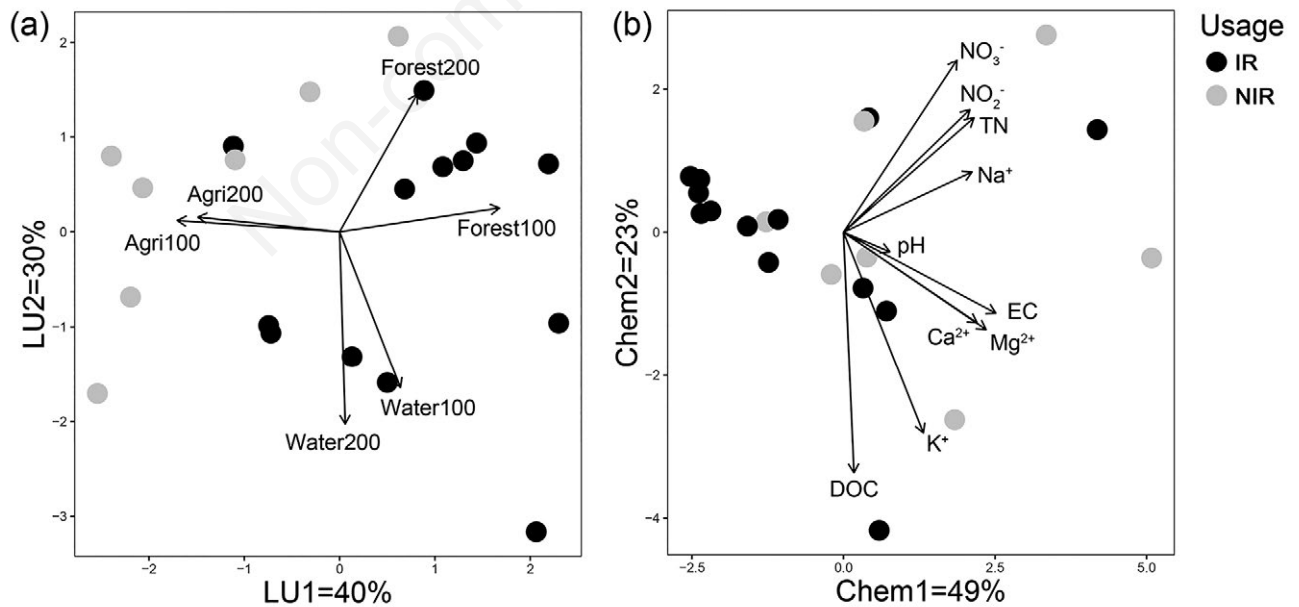


Fig. 2. Principal component analysis (PCA) results of the explanatory variables. The PCA plot of (a) land use and (b) water chemistry variables. The land use variables indicate the percentage of cover of agricultural (Agri100, Agri200), forested (Forest100, Forest2000) and water areas (Water100, Water200) within 100 and 200 m from edges of the *dumbeongs*, respectively. IR, ponds used for irrigation regularly in recent 5 years; NIR, ponds not used for irrigation for more than 5 years; TN, total dissolved nitrogen; DOC, total dissolved organic carbon; EC, conductivity.

growth form. The FG1 was characterized by the annual aquatic plant species, such as *Lemna perpusilla*, *Aneilema keisak*, and *Trapa japonica*, which have above-ground vegetative propagation (Fig. 4). The FG1 plant species typically grow near or on the water surface. The FG2 represented annual facultative wetland herbaceous plant species such as *Bidens* spp. and *Persicaria thunbergii*, reproducing by seeds (Tab. S2). The FG3 and FG4 were largely composed of facultative graminoid species, and annuals and perennials, respectively; the traits including photosynthetic pathway and seed morphology were significantly different between the groups (Tab. S2). The plant species in FG5 included perennial-emergent macrophytes that reproduce by below-ground vegetative propagules (Fig. 4). The FG5 plant species grow up to approximately 1 m above the water surface. The FG6 was composed of three woody plant species of the genus *Salix*.

Composition of plant communities of the *dumbeongs*

The plant cover variation within each plant functional group and among the management types are shown as box plots (Fig. 5). The average log-transformed percent cover of the plant functional groups, except FG1, was higher in NIR *dumbeongs* than in IR *dumbeongs*. In particular, NIR *dumbeongs* were dominated by FG5 and FG2 plants. However, only the plant cover of FG2 was statistically different between the two management types of the *dumbeongs* (Fig. 5). This is because only a few plant species in FG2, such as *P. thunbergii*, *Bidens* spp., and *Humulus japonicus*, were dominant in NIR *dumbeongs*, indicating the progression of terrestrialization. Only a few plant species were included in FG3 and FG4; however, they were more concentrated in NIR *dumbeongs*.

The RDA tri-plots represented the correlations among

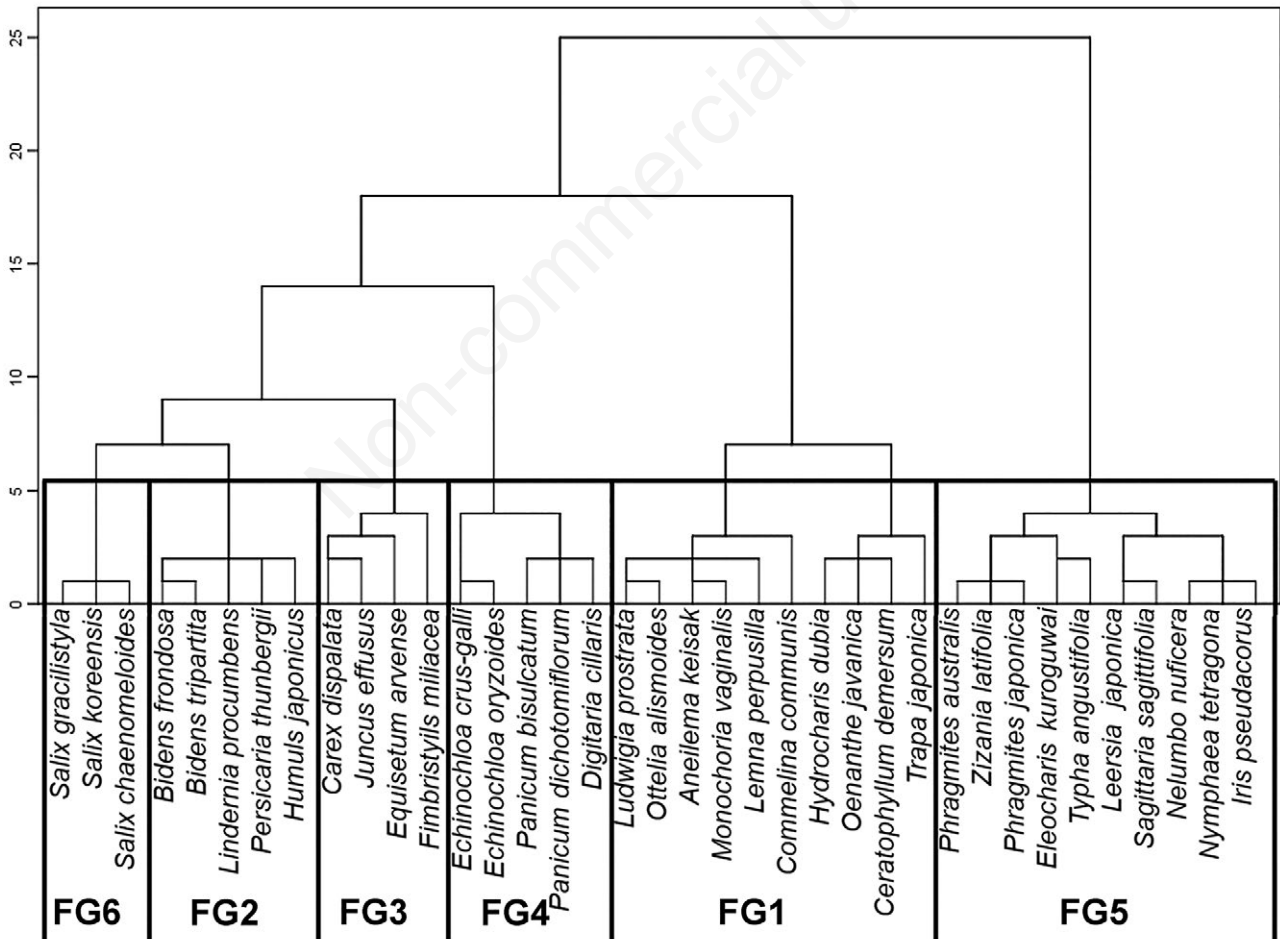


Fig. 3. Dendrogram of 37 *dumbeong* plant species based on the squared Euclidean distance of the selected traits. Six plant functional groups were classified to examine the relationships between plant community composition and explanatory variables in the *dumbeongs*.

plant communities, *dumbeongs* (plots), and explanatory variables selected by stepwise method (Fig. 6). The first two species-RDA axes explained 17% of the variation in the plant species data (Fig. 6a). The first axis of the species-RDA was primarily related to the surface area of *dumbeongs* (Tab. 4). In contrast, the depth correlated negatively with the second axis of the species-RDA. Along the first axis, *T. japonica* and *Leersia japonica* dominated some of IR *dumbeongs*; however, these plants were negatively related to the second axis. *P. thunbergii*, *Typha angustifolia*, and *Salix koreensis* grew densely along both the species-RDA axes. According to the plant functional group level, the first two RDA axes, surface area of open-water and water depth, explained 28% of the total variation in the plant communities (Fig. 6b). However, Chem2 did not exhibit statistical significance according to the randomized permutation test (Tab. 4). The functional group-RDA presented more relevant explanation than the species-RDA model (Tab. 4). The first axis of functional group-RDA correlated positively

with the surface area of open-water. The FG5 and FG1 associated negatively with this axis and this was mainly explained by the surface area of open-water. The second axis of the functional group-RDA showed a strong positive correlation with depth. According to the ordination, FG2, FG3, and FG4 dominated the shallow NIR *dumbeongs* (Fig. 6b).

DISCUSSION

Features of *dumbeongs* and adjacent land use

The land use of adjacent areas, especially within 100 m from the edge of the *dumbeongs*, was used as a determinant of irrigation usage. The water chemistry of the *dumbeongs* was affected by management practices and location. Although it was not statistically significant (Fig. S1, Fig. S2), the concentration of nutrients and the proportion of croplands and rice paddy fields within 100 m of the ponds were positively correlated as previous

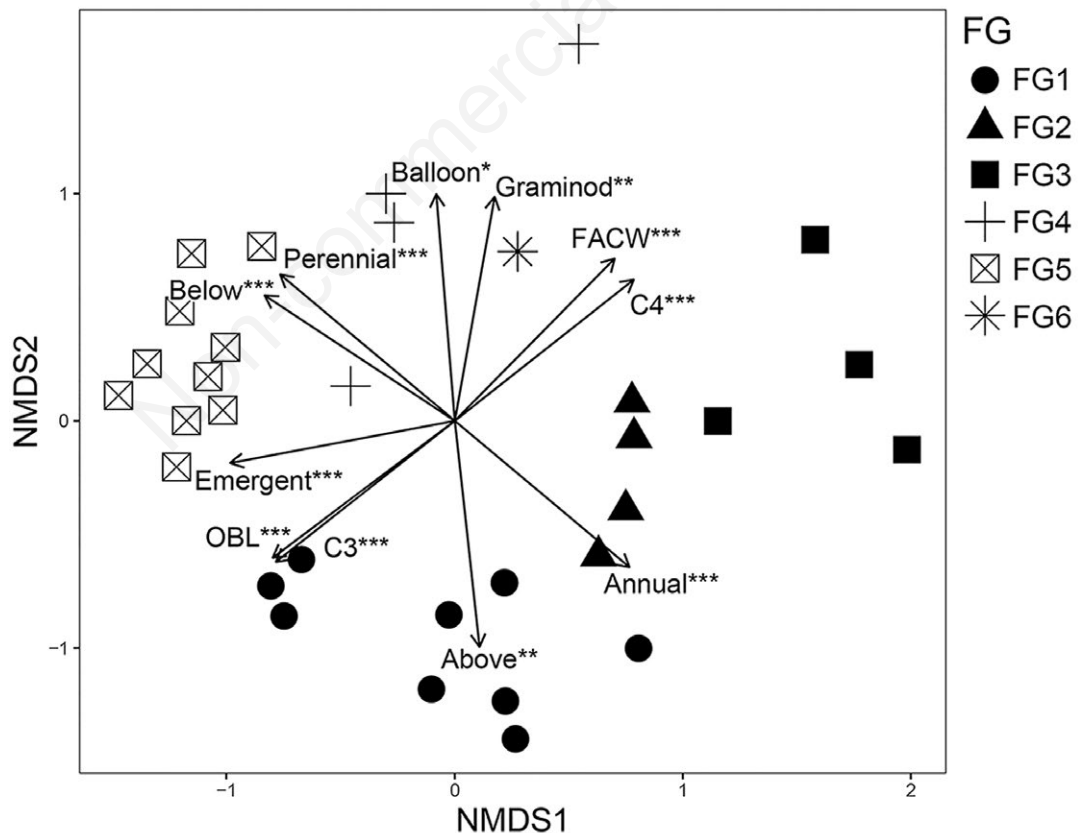


Fig. 4. Non-metric multidimensional scaling (NMDS) plot of species-trait matrix based on the Euclidean distance and fitted vectors of the selected traits. Plant species were plotted as plant functional groups (see Fig. 3). Statistically significant traits among the total selected traits were plotted. The significance of Pearson's correlation between the traits and NMDS axis scores was recorded as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. For the abbreviations of traits, please refer to Category in Tab. 1.

studies has shown (Declerck *et al.*, 2006; Akasaka *et al.*, 2010). According to the water chemistry-PCA ordination, most of the IR *dumbeongs* which were located near forested areas exhibited smaller variation and lower nutrient concentration than the NIR *dumbeongs* (Fig. 2b). These results indicate that the accumulated nutrients

were periodically removed by drainage in the IR. Furthermore, two of the IR *dumbeongs* presented unusual water chemistry. One of the IR *dumbeong* sites exhibited a high concentration of DOC and negligible nitrate and nitrite concentrations. It was completely covered with *L. perpusilla* due to the steep slope of the pond margins. As

Tab. 4. Summary of constrained ordination by RDA. The explanatory variables in the RDA results were chosen by the stepwise selection method. The assigned values of the RDA axes are the correlations between the explanatory variables and RDA axes.

Variables	RDA1	RDA2	adjR ² (%)	F	P
Plant species composition					
Area	0.80	-0.27	4	1.88	0.02
Depth	-0.22	-0.71	5	1.69	0.04
Plant functional group composition					
Open	0.57	-0.08	9	2.35	0.01
Depth	0.06	-0.61	12	2.85	0.03
Chem2	-0.26	0.31	6	2.03	0.06

Open, the percentage area of open-water surface; *Chem2*, the second principal component axis of water chemical variables (see Tab. 3, Fig. 2).

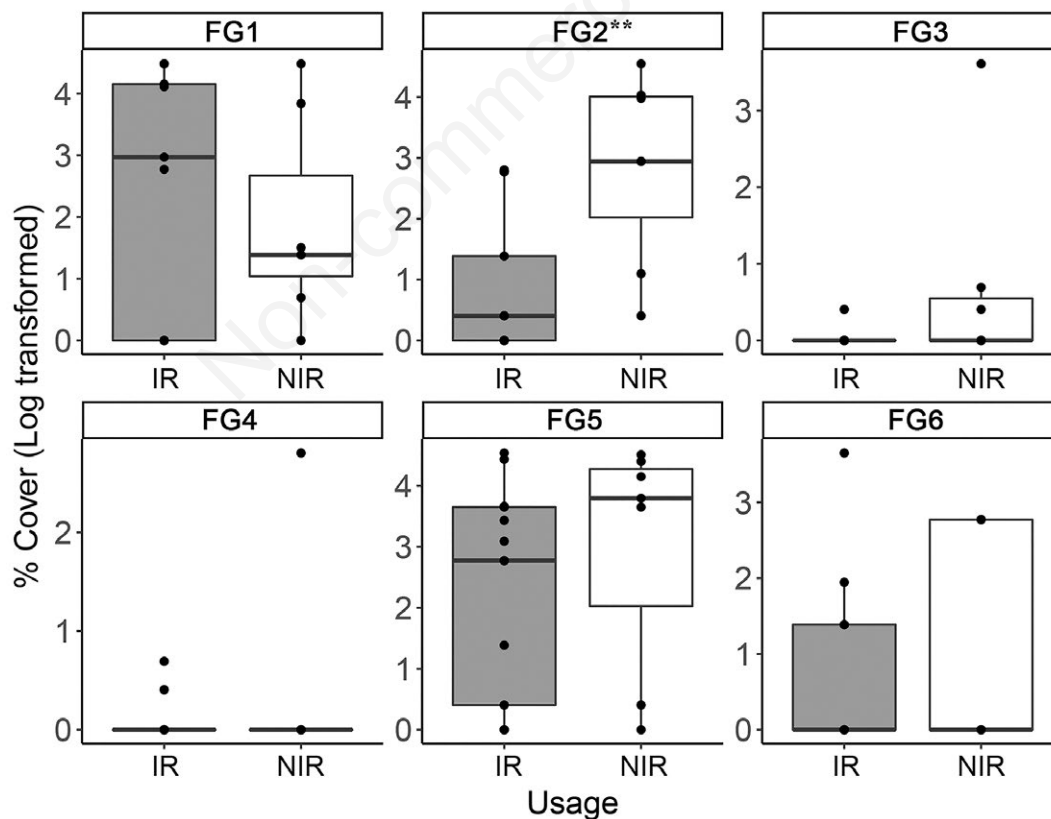


Fig. 5. Composition of the plant functional groups among the management types of the *dumbeongs*. Percentage of cover was log-transformed. The box plots represent medians (bold black horizontal line), and 25% and 75% quartiles (box perimeters). The small circles away from the vertical lines are outliers. Significant differences were tested by Mann-Whitney *U*-test (***P* < 0.01).

the site had not been used for irrigation for the past two years, the low DOC consumption rate might have resulted in the high concentration of DOC (Leenheer, 1994; Wang *et al.*, 2013). The other IR *dumbeong* site, which showed a high concentration of nitrogen nutrients, is being used as a disposal site for cow feces.

The NIR *dumbeongs* showed a higher concentration of water nutrients and a relatively wide variation in water chemistry (Fig. 2b). This variation can be explained by the difference in the location of the IR and NIR *dumbeongs*. The IR *dumbeongs* were located away from adjacent agricultural areas, at higher elevations than the cropfields or rice paddy fields for efficient water supply. Whereas, the three NIR *dumbeongs* were hydrologically connected to the paddy fields, and showed relatively high concentration of nitrogen. The difference in proximity to rice paddy fields and the output of different nutrients from the fields might have caused large variation in the water chemistry among the *dumbeongs*. Overall, the concentration of water nutrients was significantly related to the periodic usage for irrigation and the input of nutrients from adjacent rice paddy fields. However, the adjacent land use effects on pond condition was not very clear (Fig. S2). This is probably because we only considered land use in small scale areas with fixed-radius. Land use in the each pond's catchment which can reflect local characteristics such as pond area, pond topography,

and local climate should be considered in future studies (Novicmek *et al.*, 2016).

Grouping of the *dumbeong* plant species

The categorization of singular traits helps to understand complex communities with characteristics corresponding to environmental conditions (McGill *et al.*, 2006). Recent studies on the composition of plant communities in ponds have used functional categorization by traits, such as plant morphology and affinity for water, for better prediction of community composition (Gallego *et al.*, 2014; Caria *et al.*, 2015; McCann, 2015). However, over-simplification in the categorization of species limits the scope for scientific interpretation. Thus, we classified the *dumbeong* plant species according to seven response traits to reveal the relationship between the plant communities and disturbances or environmental gradients (Hooper *et al.*, 2005).

The plant functional groups were defined by traits, including life history, wetland indicator status, presence of vegetative propagules, and growth form (Tab. S2, Fig. 4). Each plant functional group is characterized by distinct dominant species. For example, FG1 is dominated by annual aquatic plants, although a few perennial plant species and one non-aquatic plant species are included (Tab. S2). The plant functional groups were classified by

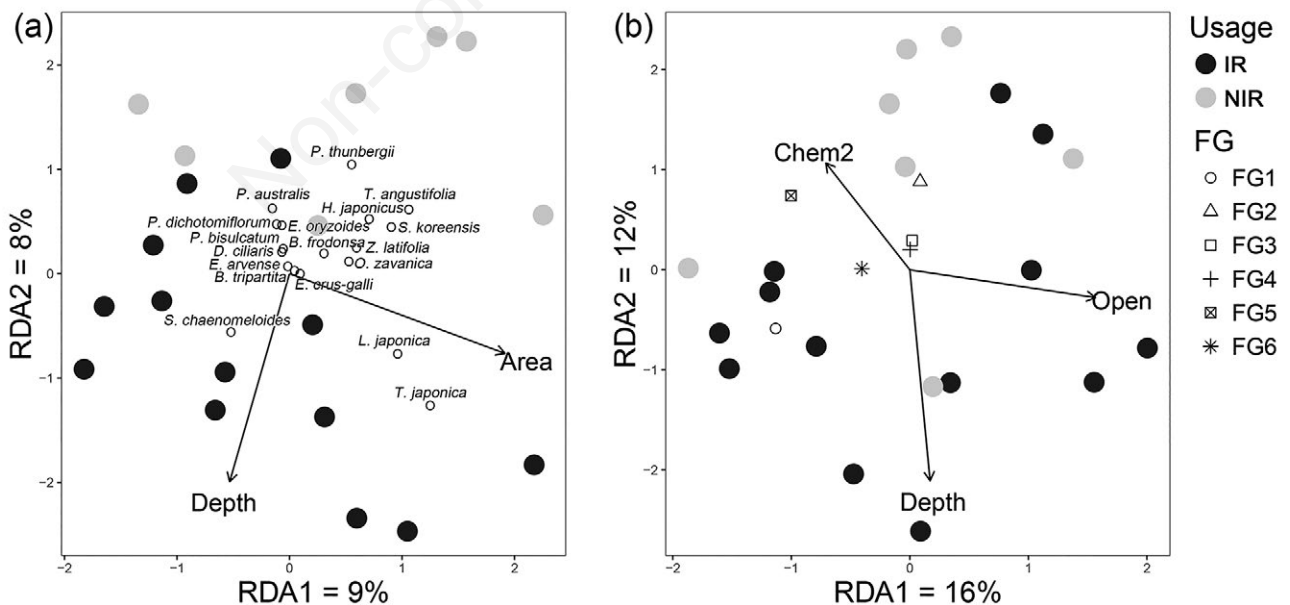


Fig. 6. Redundancy analysis (RDA) plot of (a) plant species and (b) plant functional groups. The plant species for which the RDA axes explained more than 10% of their total variation were plotted. IR, ponds used for irrigation regularly in recent 5 years; NIR, ponds not used for irrigation for more than 5 years; FG, plant functional groups (see Fig. 3); Open, the percentage area of open-water surface; Chem2, the second principal component axis of water chemical variables (see Tab. 3, Fig. 2).

the Euclidean distance to reflect ecological distance and to avoid artificial classification. Therefore, their diversity reflected the complex composition of traits within the observed *dumbeong* plant communities. While FG1 and FG5 aquatic plants that are classified as emergent species share certain similarity in terms of the growth form, it was notable that most FG1 plants tend to grow shorter than those of FG5. The use of multiple sets of traits can potentially lead to similar non-selected traits within each plant functional group. This is probably because multiple correlated traits also reveal pleiotropic changes among species (Schlichting, 1986). Nevertheless, continuous functional traits are important characteristics in a community assembly and form a basis for researchers to build quantitative prediction models in community ecology studies (Swenson and Weiser, 2010; Byun *et al.*, 2013; Laughlin, 2014). Therefore, future studies can classify the plant species by considering continuous functional traits such as specific leaf area and seed mass.

Composition of plant communities

According to the species-RDA results, area and depth were the significant predictors of plant composition in the *dumbeongs*. The area was positively correlated with *L. japonica* and *T. japonica* in the IR *dumbeongs* (Fig. 6a). The relationship between area and plant species in ponds is generally explained by the development of vegetation in the marginal area (Edvardsen and Økland, 2006). However, *L. japonica* and *T. japonica* inhabited both central and marginal areas of the *dumbeongs*, and there was no consistent co-occurrence of facultative wetland plant species, such as *P. thunbergii* and *Bidens* spp. that generally grow in the marginal spaces of ponds; the latter three species exhibited partially positive correlation with the first axis of the species-RDA in the NIR *dumbeongs* with a gentle slope formed by sedimentation over the past 10-30 years (Fig. 6b). Thus, the total surface area, size of the shallow marginal area, and development of marginal vegetation can be positively correlated in the NIR *dumbeongs*. However, the interviews with the pond owners suggested that *T. japonica* was introduced into the IR *dumbeongs* when the water was supplied from an adjacent reservoir or when the owners planted it as a food source. Because of the complexity introduced by management practices, it is thus difficult to conclude the effect of the adjacent area on the species composition of the *dumbeongs*.

At the species level, the water depth significantly negatively correlated with several species, including *P. thunbergii* and *H. japonica* (FG2), *S. koreensis* (FG6), and *T. angustifolia* (FG5). At the functional group level, FG2, FG3, and FG4 showed a convergent trend, and were similarly negatively correlated with the depth of water (Fig. 6b). Thus, the depth of water explained the variation

in the plant functional groups mainly by predicting the convergent trend according to the three functional groups, which were largely represented by early-succession plant species in the abandoned rice paddies (Lee *et al.*, 2002). Conversely, FG5 and FG6 were more significantly associated with the open-water surface area than with the water depth. Generally, in abandoned rice paddy fields, the perennial-aquatic plant species (FG5) and *Salix* species (FG6) represented the plant communities at the intermediate and later stages of succession, respectively (Lee *et al.*, 2002).

Our results showed that the plant communities of NIR *dumbeongs* were in the process of succession. Although the water depth and plant cover of FG5 significantly differed between IR and NIR *dumbeongs*, the plant functional group-RDA model exhibited a low correlation between depth and FG5 (Fig. 6b). There are two possible explanations for this result. First, the typical plant species in FG5 easily occupy wetlands through vegetative propagation (Boutin and Keddy, 1993; Mitsch *et al.*, 2012; Sayer *et al.*, 2012). Second, transplantation was prevalent among the pond owners, which seemed to affect the plant community composition. For example, six species, including two *Salix* species, *T. japonica*, *Nelumbo nucifera*, *Nymphaea tetragona*, and *Iris pseudacorus*, were intentionally planted for various purposes (Tab. S3). In particular, three planted species of floating-leaved macrophytes with large leaves and four species that rapidly reduce the open-water area of *dumbeongs* belonged to FG5. Furthermore, FG1 plants, including *T. japonica* and fast-growing annual aquatic plant species, dominated some of the IR *dumbeongs* (Figs. 5 and 6).

The open-water surface area is not an environmental filter that determines the composition of plant communities (Van der Valk, 1981; Keddy *et al.*, 1992). However, studies have discussed the importance of maintaining moderate levels of open-water to allow aquatic insects to breed and to retain the diversity of plants (Chester and Robson, 2013). Extremely large surface areas of water, as frequently observed in IR *dumbeongs*, lack shelter and breeding places for amphibians and macroinvertebrates (Gioria *et al.*, 2010; Landi *et al.*, 2012). Although planting can increase the diversity of plant species, it can lead to low alpha diversity of macrophyte species due to shading (Hassall *et al.*, 2011; Sayer *et al.*, 2012; Pier *et al.*, 2015). Thus, proper management is required to enhance biodiversity by controlling some FG1 and FG5 plant species that are well adapted to environmental disturbances.

Studies have discussed the influence of water chemistry on the composition of plants in ponds (Capers *et al.*, 2010; Del Pozo *et al.*, 2010; Kim *et al.*, 2011). Our findings showed that the concentration of water nutrients was relatively high in IR *dumbeongs*, however, there is a

marginal relationship between water chemistry and plant composition. Although Chem2, which was selected in the stepwise selection method when we developed RDA models, presented large variation in DOC and NO_3^- among NIR *dumbeongs* (Fig. 2b), the difference was not significant in the post-hoc test (Tab. 4). Thus, environmental filtering by water chemistry did not significantly affect the *dumbeong* plant composition.

Our study identified three types of plant communities in five NIR *dumbeongs* that contained no introduced plant species: (1) FG2 dominant, (2) FG5 dominant, and (3) FG3 and FG4 dominant. The concentration of NO_3^- was considerably lower (about one-tenth) in types (1) and (3), than in type (2). However, each functional group was composed of wetland plant species related to different ranges of water quality conditions. For example, in FG5, *T. angustifolia*, *Sagittaria sagittifolia*, and *L. japonica* are indicators of nutrient-rich habitat, whereas *Phragmites japonica* and *Eleocharis kuroguwai* are sensitive to eutrophic conditions (Penning *et al.*, 2008; Seo *et al.*, 2014). As we did not select the functional traits representing nutrient conditions, the effect of Chem2 as an environmental filter on plant community composition at functional group levels was blurred. Furthermore, the species planted by the pond owners, regardless of the nutrient conditions, cannot be ignored. Consequently, the physiochemical environment and plant communities across the *dumbeongs* appeared to be independently determined by anthropogenic influences, especially the use of adjacent land and ponds for irrigation.

CONCLUSIONS

Management practices affected the environment and plant composition of *dumbeongs*. The use of *dumbeongs* for irrigation generally prevented the accumulation of nutrients that might have made the ponds shallow. However, extremely high nutrient accumulation was detected in the IR *dumbeongs*, owing to the non-conventional management practices. In contrast, the NIR *dumbeongs* were more affected by land use in the adjacent rice paddies than by the management practices of the *dumbeongs*. Although the composition of plant species and plant functional groups did not correlate with the water chemistry variables, the predictors explained more variation in the plant functional groups than in the plant species.

Our approach showed that the plant functional groups predict plant composition in the *dumbeongs* better than the plant species. One limitation of the study is that only a few characteristics of the plant functional groups, representing the degree of adaptation to aquatic conditions, were strongly related to plant composition of the *dumbeongs*. Thus, future studies should consider continuous functional traits when building plant

functional groups to better understand the composition of plant communities and to develop an appropriate conservation plan for *dumbeongs*.

Overall, the findings of the present study show that management practices, including irrigation usage, planting, and plant removal, are crucial to improve the ecological function of *dumbeongs* as wetland habitats in the agricultural landscapes in Korea. In addition, analysis based on plant functional groups rather than plant species can be more applicable in the management of biodiversity in *dumbeongs*, as it can provide a clear view of the ecological niche of plant communities in *dumbeongs*.

ACKNOWLEDGMENTS

The present study was supported by the Basic Science Research Program through the National Research Foundation of Korea, funded by the Ministry of Science, ICT, and Future Planning (grant number NRF-2015R1A2A2A03007350). The functional trait data of our study has been supported by the TRY initiative on plant traits (<http://www.try-db.org>). This initiative and database is hosted, developed and maintained by Jens Kattge and Gerhard Bönisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY has been supported by DIVERSITAS core project bioDISCOVERY, the IGBP, the Global Land Project, the UK Natural Environment Research Council (NERC) through its program QUEST (Quantifying and Understanding the Earth System) and the French programs 'Climat, Environnement, Société', and the French Foundation for Biodiversity Research (FRB). We appreciate all the owners of *dumbeongs* who allowed us to investigate their ponds. We are also grateful to Yuri Cho, Minjoo Lee, Minji Son, and Bumsuk Seo for helpful advice on the manuscript. Finally, the authors thank Junyong Song, Donguk Han, Eunjeong Lee, Eunju Lee, Hyunyoung Chung, and Minjeong Cha for their great help with field and laboratory work.

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