A study of the relationship between wetland vegetation communities and water regimes using a combined remote sensing and hydraulic modeling approach

Tan Zhiqiang, Zhang Qi, Li Mengfan, Li Yunliang, Xu Xiuli and Jiang Jiahu

ABSTRACT

Hydrologic condition is a major driving force for wetland ecosystems. The influence of water regimes on vegetation distribution is of growing interest as wetlands are increasingly disturbed by climate change and intensive human activities. However, at large spatial scales, the linkage between water regimes and vegetation distribution remains poorly understood. In this study, vegetation communities in Poyang Lake wetland were classified from remote sensing imagery. Water regimes characterized by inundation duration (IDU), inundation depth (IDE), and inundation frequency were simulated using physics-based hydraulic models and were then linked with vegetation communities by a Gaussian regression model. The results showed that the *Carex* community was found to favor more hydrologic environments with longer IDU and deeper IDE in comparison to the *Phragmites* community. In addition, we found that the *Carex* community could survive in a relatively wider variety of hydrological conditions than the *Phragmites* community. For the typical sub-wetlands of the Poyang Lake National Nature Reserve (PLNNR), only the influence of IDU on the distribution of vegetation communities was significant. Outcomes of this research extend our knowledge of the dependence of wetland vegetation on hydrological conditions at larger spatial scales. The results provide practical information for ecosystem management.

Key words | hydraulic modeling, Poyang Lake wetland, remote sensing, vegetation community, water regime

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INTRODUCTION

Wetland ecosystems are dynamic and diverse landscapes in not only their spatial scale, but also their hydrological conditions and vegetation communities. Understanding the relationships between vegetation distribution and hydrologic conditions can assist in more effective management of wetlands. As a key component of wetlands, wetland plant communities vary spatially with the type of climate (Piao *et al.* 2004; Liu *et al.* 2013), soil (Sanderson *et al.* 2008; Xu *et al.* 2013; Wang *et al.* 2014) and, in particular, the characteristics of water regime in terms of inundation duration (IDU), inundation depth (IDE), and inundation frequency (IFR) (Stromberg *et al.* 1996; Toogood & Joyce 2009). Water regime is a primary factor influencing the composition, productivity, stability, species diversity, and succession of a wetland vegetation community. This factor acts as an environmental sieve that interacts with life history characteristics of plant species (Van der Valk 1981; Gerritsen & Greening 1989).

Numerous studies of individual species have shown different responses to the effects of different aspects of water regimes

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(e.g., Denton & Ganf 1994; Rea & Ganf 1994; Van den Brink *et al.* 1995). For example, Casanova & Brock (2000) suggested that IDU, rather than IDE and IFR, is the most important aspect of the water regime in segregating vegetation communities. Todd *et al.* (2010) linked hydrological dynamics with vegetation distribution across Everglades National Park, indicating that IDU and IDE are the principal structuring variables to which individual communities respond.

Controlled experiments have been performed to identify key hydrologic requirements for species under specified conditions (Newbold & Nature 1997). However, other researchers have concluded that controlled experiments have limitations in their ability to predict species presence or abundance in field settings (Silvertown *et al.* 1999). Hence, there is a strong need for a typical ecosystem to reflect the relationship of vegetation with associated water regime.

The extensive wetland developed by the intra/inter-annual water-level fluctuations of Poyang Lake offers a reference site to study this relationship. The ecological and environmental conditions of Poyang Lake have been changing rapidly due to climate change and human activities, and the water level has declined significantly over the last decade (Zhang *et al.* 2012b). As the largest freshwater lake in China, Poyang Lake's hydrologic characteristics depend on both inflow from tributaries and outflow into the Yangtze River, which is affected by river discharge and the water level (Shankman & Liang 2003; Li & Zhang 2015). The construction of the Three Gorges Dam (TGD, the biggest concrete dam in the world), which began to impound water on 1 June 2003, has been suggested as a causal factor for the decline in the water level of Poyang Lake (Feng *et al.* 2013; Lai *et al.* 2014). Since 2003, the effects of the TGD pilot impoundment on the regional hydrology (Guo *et al.* 2012; Mei *et al.* 2015), environment (Zhao *et al.* 2013), and ecosystem (Yi *et al.* 2010; Fang *et al.* 2012) have begun to emerge. Changes in climate (Guo *et al.* 2008; Tao *et al.* 2014) and other human activities (de Leeuw *et al.* 2010; Ye *et al.* 2013) have also dried out the Poyang Lake wetland.

Consequently, the altered hydrology could result in a potential change in the plant community (Toogood *et al.* 2008). Any change will be mediated through species traits or attributes that establish niche and competitive abilities of particular species (Keddy 1992). The effects are greatest in shallow water, where even small changes in lake level can result in conversion of a standing water environment to an environment in which sediments are exposed to the air, or vice versa, resulting in death by flooding or in plant seeding-bank germination (Keddy & Reznicek 1986). For instance, Yu *et al.* (2010) suggested that the Ganjiang delta has expanded toward the main body of Poyang Lake, a movement that was obviously influenced by the variation in water level. In addition, species traits persist in successful adaptations to the environment and competition can be used to classify ecological groups of species (Boutin & Keddy 1993; Hu *et al.* 2015). Therefore, a better understanding of the patterns of vegetation distribution involved with the changed water regimes is essential for wetlands management.

The effects of variable hydrological processes on vegetation distribution have been investigated previously in the Poyang Lake wetland. However, most studies of hydrology and vegetation structuring have taken place in relatively narrow spatial scales, from a belt less than 1 km^2 (Xu *et al.* 2014) and a typical sub-lake of up to tens of km^2 (Wu *et al.* 2010), to a reserve of hundreds of km^2 (Zhang *et al.* 2012a). The Poyang Lake wetland is a highly dynamic and diverse area with abundant vegetation communities along different hydrological gradients. Previous methods, such as controlled experiments and field surveys, are not available that reflect the spatial heterogeneity of the hydrologic and vegetation conditions of the entire wetland over the same period in time. Different sampling dates and investigation methods lead to different conclusions (e.g., Ge *et al.* 2011). Even if some researchers have carried out studies on the entire Poyang Lake wetland, quantitative relationships between specific water regimes and the distribution of dominant communities have not been well documented (e.g., Zhang *et al.* 2013).

To the best of our knowledge, remote sensing data with high spatial resolution provides a consistent and rapid measurement of vegetation conditions. Moreover, hydrodynamic/hydrologic models provide the most accurate method to identify the hydrologic conditions of a large area. Given this background, a combined approach of remote sensing and hydrodynamic modeling was applied to reveal the relationship between water regimes and the spatial patterns of communities in the entire Poyang Lake wetland. The objectives of this study were to: (1) identify the hydrological preferences of different plant communities over the entire Poyang Lake wetland and (2) evaluate the individual and combined effects of water regimes on patterns of community distribution.

MATERIALS AND METHODOLOGY

Study area

Located in the middle and lower reaches of the Yangtze River, Poyang Lake (N28°24′–29°46′, E115°49′–116°46′) receives inflow from five major rivers (Ganjiang, Fuhe, Xinjiang, Raohe, and Xiushui) and eventually discharges into the main stream of the Yangtze River at Hukou (Figure 1). In response to the annual cycle of precipitation, water flows from the Poyang Lake basin have an annual course, with large runoff inflow starting in February and peaking

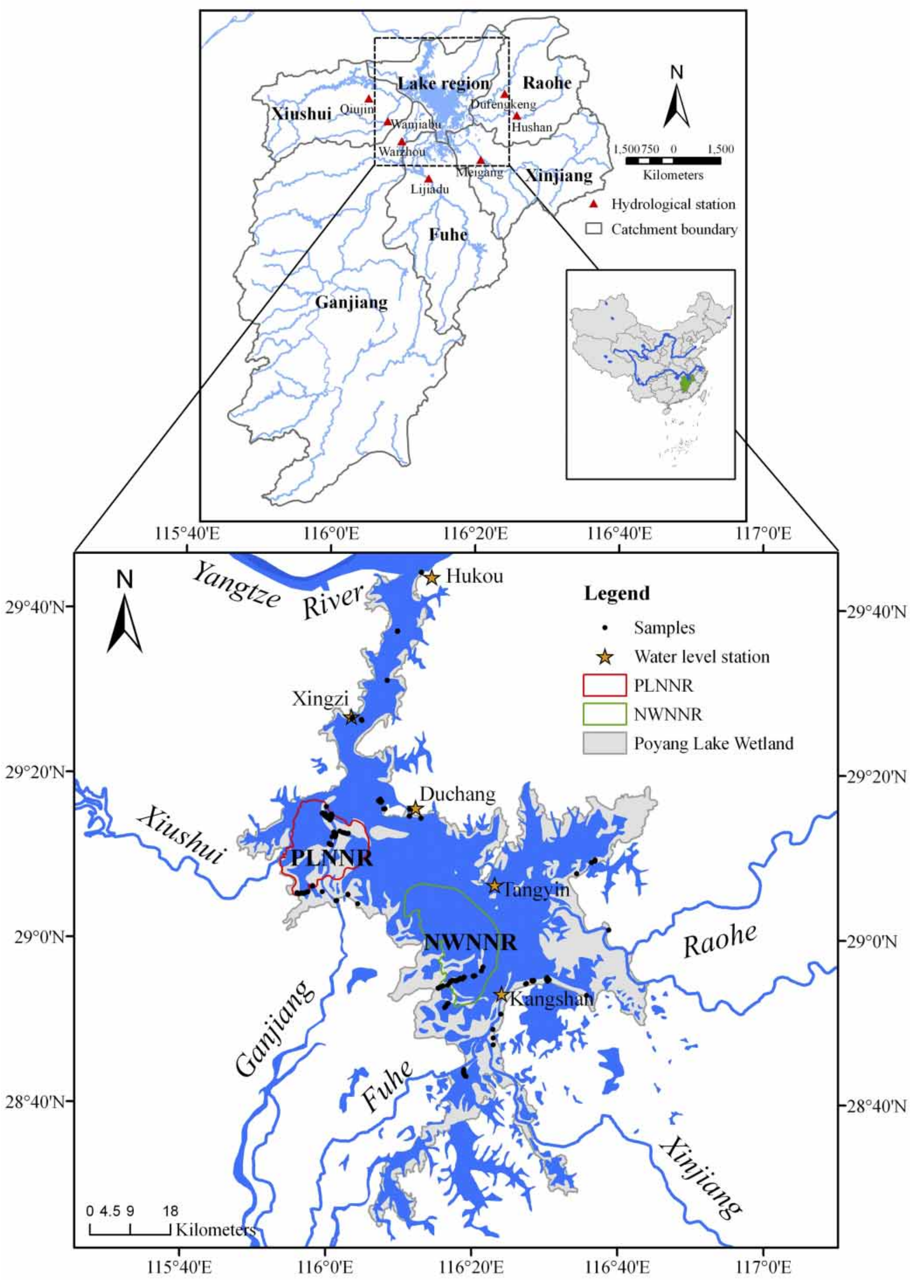

Figure 1 | Geographical location of the Poyang Lake wetland as well as samples, nature reserves, and gauging stations. PLNNR: Poyang Lake National Nature Reserve; NWNNR: Nanji Wetland National Nature Reserve.

from April to June (Hu *et al.* 2007). A considerable variation of some 10 m in the lake water level occurs as a result of the combined effects of catchment inflows and interaction with the Yangtze River (Zhang *et al.* 2014). In the flood season, almost all floodplains are inundated and the lake scale reaches >3,000 km^2. In the dry season, the lake can be less than 1,000 km^2 in scale, with only several wandering water courses remaining (Feng *et al.* 2011). An extensive wetland is developed by the dramatic water-level fluctuations of the Poyang Lake. The Poyang Lake wetland is famous for its abundant biodiversity and was registered as one of the world's most important wetlands in 1992. It provides vital habitats for many species, including some rare and endangered birds, such as the swan goose (*Anser cygnoides L.*), and 95% of the entire world population of Siberian crane (*Grus leucogeranus Pallas*) (Wu *et al.* 2009).

Depending on the water level and other environmental conditions, wetland vegetation in Poyang Lake exhibits zonal distribution from the lake center to the shorelines. The primary vegetation zones include floating vegetation zone (e.g., *Trapa bispinosa* and *Nymphoides peltata*), submerged vegetation zone (e.g., *Potamogeton malaianus*, *Vallisneria spiralis*, and *Hydrilla verticillata*), emergent aquatic vegetation zone (e.g., *Carex cinerascens* and *Phalaris arundinacea*), semi-aquatic emergent tall vegetation zone (e.g., *Phragmites communis*, *Triarrhena lutarioriparia*, and *Zizania latifolia*), and mesophytic vegetation zone (e.g., *Artemisia selengensis* and *Cynodon dactylon*). *Carex* and *Phragmites* are the most widespread vegetation communities in the Poyang Lake wetland (Guan *et al.* 1987; Ge *et al.* 2011).

The primary *Carex* spp. (including *Carex cinerascens*, *Carex argyi*, and *Carex unisexualis*) can grow both in shallow water and wet soil. Another species – *Phalaris arundinacea* – is difficult to distinguish from *Carex* in remote sensing imagery. Therefore, both are classified into the *Carex* community in this study. The *Carex* community provides an ideal place for migratory birds to spawn, rest, feed, and avoid predators. It also supplies local residents with fuel, fertilizer, and grass. *Phragmites* is another important wetland community and usually mix with *Triarrhena lutarioriparia* and *Artemisia selengensis*. *Phragmites* communities provide food and habitat for wintering migratory birds, and their height also protects the migratory birds from human interference (Sang *et al.* 2014). The detailed composition of three typical communities within Poyang Lake wetland can be found in Table 1.

Table 1 | Species composition of the three typical communities within Poyang Lake wetland

	Species	
Communities	Dominant	Companion
Carex	*Carex cinerascens*, *Carex doniana*, *Carex laticeps*, *Carex unisexualis*, *Carex argyi* and *Phalaris* spp.	*Phragmites* spp., *Artemisia argyi*, and *Polygonum hydropiper*
Phragmites	*Phragmites* spp. and *Triarrhena lutarioriparia*	*Polygonum hydropiper*, *Acorus calamus*, *Juncus* spp., *Carex* spp. and *Cyperus* spp.
Artemisia	*Artemisia capillaris*, *Cynodon* spp. and *Conyza canadensis*	*Dicranopteris* spp., *Pennisetum* spp., *Artemisia selengensis* and *Echinochloa crusgali*

Note: Communities are defined by their dominant species, covers of which are greater than 50%.

Vegetation database

Owing to the flat terrain and fertile sediment, the alluvial plains maintain high plant species richness and diversity. Since the area of exposed grassland reaches a maximum in winter, the land surface conditions of the Poyang Lake wetland were derived using a December 24, 2013 Landsat 8 remote sensing image (LC81210402013358LGN00) with a spatial resolution of 30 m.

In the field survey, 259 test samples were collected in December 2013 coinciding with the satellite overpass (Figure 1). Sample sites were chosen mainly from the Poyang Lake National Nature Reserve (PLNNR), the Nanji Wetland National Nature Reserve (NWNNR), Kangshan, Baishazhou, and Duchang. In view of the spatial resolution of the Landsat 8 image (30 m), 10 types of land cover were defined: water, swamp, forest, mudflat, meadow, sparse grass, bare land, arable land, sand, and specified plant species (e.g., *Carex cinerascens*, *Phalaris arundinacea*, *Phragmites communis*, *Triarrhena lutarioriparia, Artemisia selengensis*, etc.). Considering the zonal distribution of the plant communities corresponding to the variation in elevation, field sampling was conducted perpendicular to vegetation zones to collect different species, and parallel to the shore of the lake to collect more samples from the same community. The individual community composition was assessed from a 1 × 1 m plot when the cover of the dominant plant species was greater than 50%. All sampling data were recorded by GPS for later image classification and accuracy assessment.

Object-based image analysis

In this study, we applied object-based image analysis (OBIA) to examine the broad-scale composition of the general surface cover types of the Poyang Lake wetland. OBIA has been applied frequently and widely for image classification in wetlands and inundation systems (Desclée *et al.* 2006; Conchedda *et al.* 2008; Laba *et al.* 2010). Compared to pixel-based image analysis, OBIA adds object shape and context (e.g., neighborhood characteristics) to spectral and textural information in the analysis, which makes OBIA an exceptionally useful method for wetland studies (Johansen *et al.* 2007; Dronova *et al.* 2011).

First, we rejected non-vegetation pixels by specifying a threshold value of the normalized difference vegetation index (NDVI) in ENVI 4.8 (ITT Inc.). Second, groups of pixels at desired scale, shape, and compactness criteria were segmented into objects in ENVI EX 4.8. In order to select the most suitable segmentation, we assessed the output sensitivity to multiple combinations of shape, scale, and compactness. Third, based on the sampling data and field survey experience, we classified the segments into categories of interest by supervised classification. Finally, individual plant species were merged into specified communities; spatial distribution and quantitative evaluation were conducted in ArcGIS 9.3 (ESRI Inc.). Classification uncertainty was examined by a fuzzy set-based accuracy assessment.

MIKE 21 HD

Lake water levels were obtained for five gauging stations (Hukou, Xingzi, Duchang, Tangyin, and Kangshan) from the Hydrological Bureau of Jiangxi Province and the Hydrological Bureau of the Yangtze River Water Resources Commission (Figure 1 and Table 2). The limited amount of observed data did not reflect the hydrological information of the entire wetland, especially for the dish-shaped pit groups (a large quantity of special geomorphic units) and the nature reserves due to the coarse spatial resolution. Accordingly, the water level information for the Poyang Lake wetland was simulated using a 2D depth-averaged hydrodynamic model, which was implemented previously

Table 2 | Hydrological gauging stations used in this study

Gauging station	Data description	Coordinates	Location	Gauged area (km²)	Period
Qiujin	Catchment inflow	(115.41°, 29.10°)	Xiushui	9,914	2006–2012
Wanjiabu	Catchment inflow	(115.65°, 28.85°)	Liaohe tributary of Xiushui	3,548	2006–2012
Waizhou	Catchment inflow	(115.83°, 28.63°)	Ganjiang	80,948	2006–2012
Lijiadu	Catchment inflow	(116.17°, 28.22°)	Fuhe	15,811	2006–2012
Meigang	Catchment inflow	(116.82°, 28.43°)	Xinjiang	15,535	2006–2012
Hushan	Catchment inflow	(117.27°, 28.92°)	Le'an tributary of Raohe	6,374	2006–2012
Dufengkeng	Catchment inflow	(117.12°, 29.16°)	Changjiang tributary of Raohe	5,013	2006–2012
Hukou	Inflow/outflow- water level	(116.22°, 29.75°)	Outlet of Poyang Lake	162,225	2006–2010
Xingzi	Lake water level	(116.03°, 29.45°)	Lake downstream	–	1960–2012
Duchang	Lake water level	(116.18°, 29.27°)	Lake midstream	–	1960–2012
Tangyin	Lake water level	(116.23°, 29.06°)	Lake midstream	–	1960–2012
Kangshan	Lake water level	(116.42°, 28.88°)	Lake upstream	–	1960–2012

by Li *et al.* (2014) using the MIKE 21 code (DHI 2007). The MIKE 21 code has been extensively applied in studying various water bodies around the world (Martinelli *et al.* 2010; Schoen *et al.* 2014).

The model covers an area of 3,124 km^2, which was determined by examining the historic lake surface during periods with high water levels. A 2D grid system with an unstructured triangular grid was adopted to capture the complex bathymetry of Poyang Lake (surveyed in 1998 and updated with new data obtained in 2000). The size of mesh elements varied from 70 to 1,500 m, resulting in a total of 20,450 triangular elements. The time step was set to 5 s to limit the Courant–Friedrich–Levy number for a stable solution.

Observed daily inflows from the five main rivers (monitored by seven gauging stations) were input into the lake model, specified as upstream boundary conditions. Meanwhile, observed daily water levels of Hukou were specified as the downstream boundary. Runoff from the ungauged catchment area was calculated using a simple linear extrapolation of the gauged runoff, and was added to the gauged inflows. For the periodically inundated wetlands, an option in MIKE 21 was used, which accounted for incidental rainfall at all model elements, whereas evaporation only applied to the wet elements representing the inundated area. For dry elements, it was assumed in the model that all rainfall was transformed to surface runoff. The numerical option of wetting and drying in the hydrodynamic model was well suited to the considerable variations in the lake water surface area in response to water-level fluctuations (Li *et al.* 2014).

Tabacchi (1995) argued that plant communities were more likely to reflect a response to water regime history than to the existing water regimes at the time of survey. In view of the considerable lag in vegetation change in response to hydrologic alterations (Ross *et al.* 2003; Givnish *et al.* 2008), the variation of historical lake water levels for Duchang during 2000–2012 was detected using the BFAST (Breaks for Additive Seasonal and Trend) method (Verbesselt *et al.* 2010a, 2010b). Duchang station is located in the central part of the lake, and was expected to reflect the average condition of the water regime for the lake (Figure 2). One break point was detected in July 2003. The confidence interval indicated that regime shift might have occurred from December 2002 to May 2005. Variation of the water level during 2006–2012 was relatively smooth, thus, hydrological information for this period was simulated by MIKE 21.

According to the requirements of this study, nodal water levels, total depth, and the outflows at Hukou were output from the model. The simulated results of the MIKE 21 were validated against the observed water level (for Xingzi, Duchang, Tangyin, and Kangshan) and discharge (for Hukou) for the periods of 2006–2012 and 2006–2010, respectively (Figure 3 and Table 3). Simulated water level and discharge were evaluated by three evaluation criteria include the Nash–Sutcliffe efficiency coefficient (E_{ns}), determination coefficient (R^2), and relative error (Re) (Li *et al.*

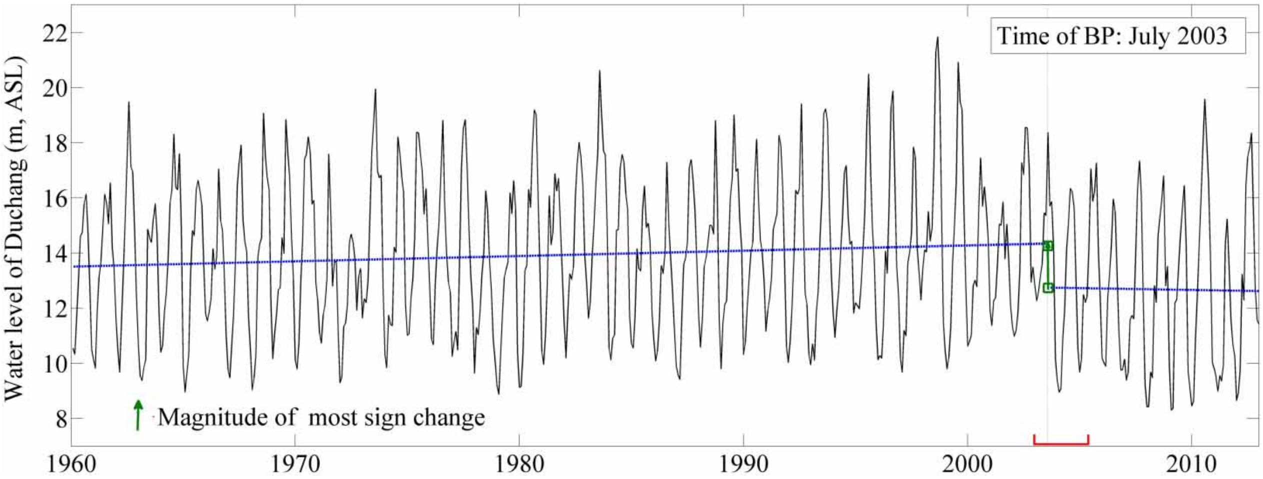

Figure 2 | Linear trend and change point for the Duchang water level series (1960–2012). The short horizontal line at the bottom shows the confidence interval of the change time. BP: break point.

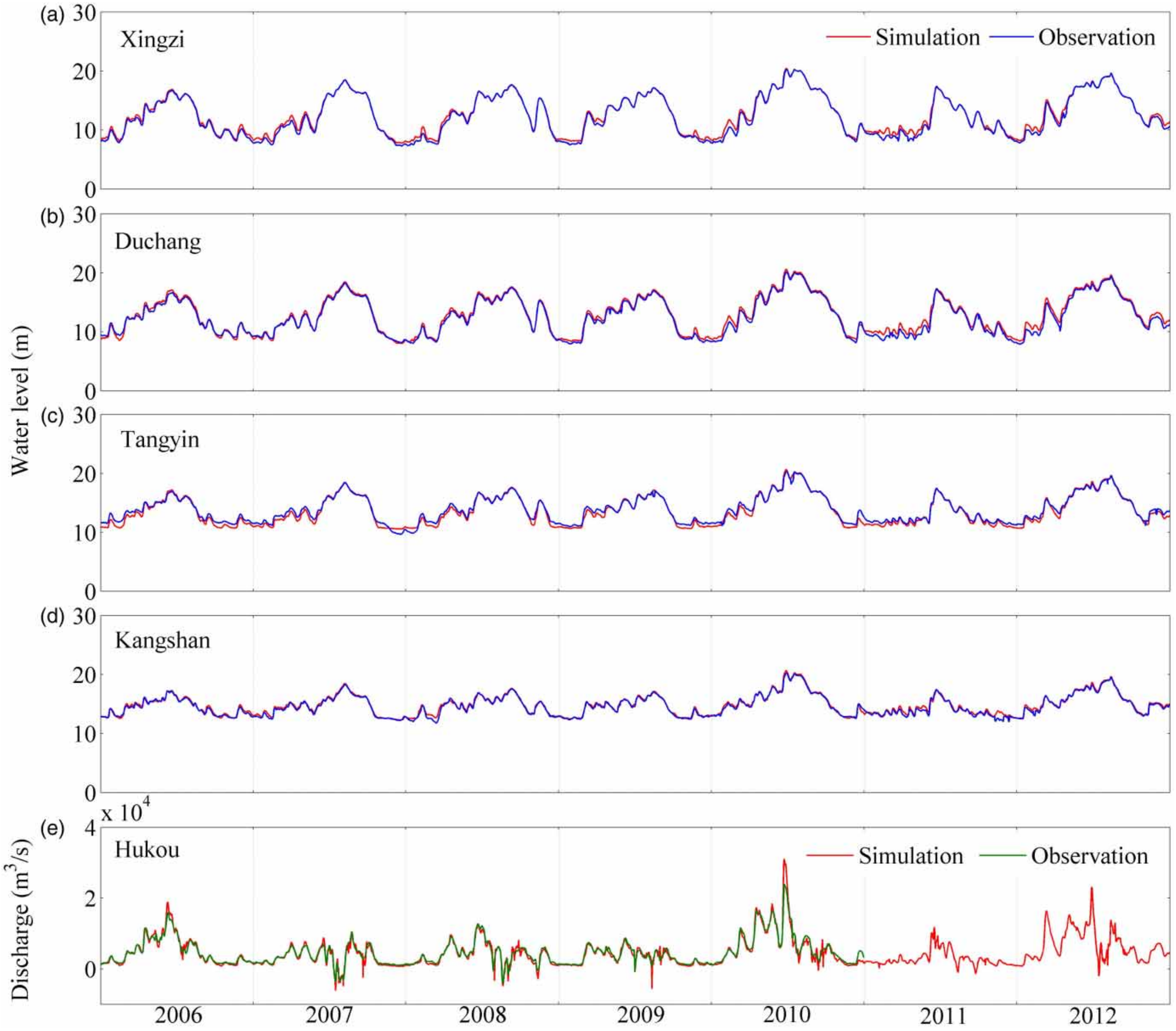

Figure 3 | Comparison of observed and simulated results: (a), (b), (c), and (d) the lake water levels at Xingzi, Duchang, Tangyin, and Kangshan, respectively; (e) the observed (during 2006–2010) and simulated outflow (during 2006–2012) at Hukou.

Table 3 | Quantitative assessment of model validation for MIKE 21

Gauging stations	**Calculation Indexes**	**Validation period**	**Performance**		
			E_{ns}	R^2	*Re*
Xingzi	Water level	2006–2012	0.98	0.99	0.02
Duchang	Water level	2006–2012	0.98	0.99	0.03
Tangyin	Water level	2006–2012	0.95	0.98	−0.02
Kangshan	Water level	2006–2012	0.98	0.98	0.01
Hukou	Discharge	2006–2010	0.93	0.95	−0.04

2015). E_{ns} and R^2 were all above 0.93, and the absolute values of *Re* were below 0.05, indicating a satisfactory model calibration (Table 3). To depict the regimes in terms of water inundation, IDU was defined as the number of inundation days each year. The IDE was calculated as the mean depth of all inundated days. In order to distinguish the ecological significance of IDU, the IFR was defined as the number of times each pixel was inundated in a year, which reveals the water surface submersion and exposure processes of lake expansion and shrinkage in different zones.

Gaussian regression model

The Gaussian regression model is available for evaluating the normal distribution of a vegetation population along environmental gradients (Gause 1931). The model can be expressed as:

$$y = c\ \exp\left[-\frac{1}{2}\frac{(x-u)^2}{t^2}\right] \tag{1}$$

where y is the richness of vegetation, and it is derived from the abundance (relative coverage) of each community within each gradient of water regimes; x is the environmental indices, which contains IDU, IDE, and IFR in this paper; c is the maximum of richness, u is the optimum environment, which appears when y equals c; and t is the tolerance range of the vegetation, and it refers to the capacity of communities to endure the water regimes (IDU, IDE, and IFR) in this study (Figure 4).

RESULTS

Vegetation

In order to account for the high spatial heterogeneity of the Poyang Lake wetland, the interpretation precision of cover types was analyzed by a fuzzy set-based accuracy assessment.

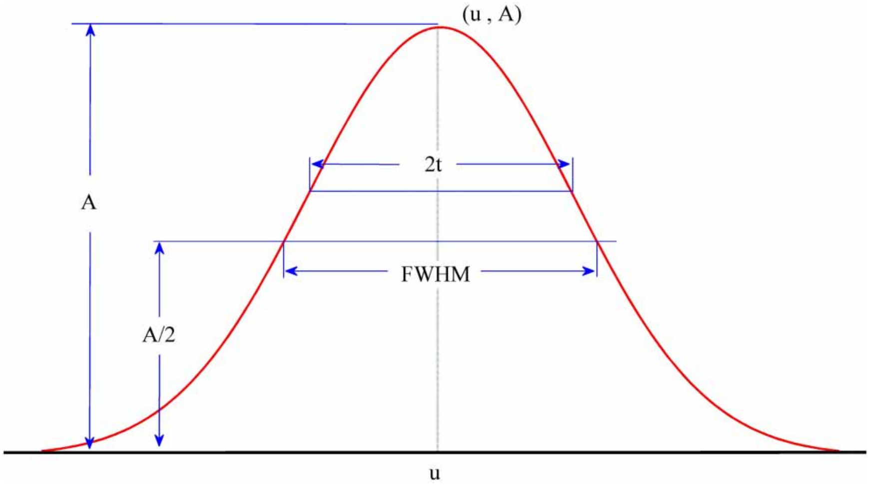

Figure 4 | Sample curve of Gaussian regression.

Table 4 | Fuzzy accuracy assessment for the interpretation results of major cover types in the Poyang Lake wetland

Classes	Swamp	Forest	Mudflat	Meadow	Sparse grass	*Carex* community	Bare land	*Artemisia* community	*Phragmites* community	Sand	Omission
Swamp	79.71	0	8.05	0	0	0	0	0	0	0	20.29
Forest	1.45	79.31	0	0	9.28	0	0	0	0	0	20.69
Mudflat	10.14	0	82.76	6.00	10.31	0	0	0	0	0	17.24
Meadow	4.35	1.72	5.75	84.00	0	2.06	0	4.85	1.55	0	16.00
Sparse grass	4.35	17.24	3.45	0	73.20	4.94	1.49	5.29	0.67	0	26.80
Carex community	0	1.72	0	3.00	3.09	89.30	0	7.93	2.88	0.70	10.70
Bare land	0	0	0	0	0	0	74.63	0	0	2.81	25.37
Artemisia community	0	0	0	6.00	3.09	2.47	10.45	81.50	0.22	3.51	18.50
Phragmites community	0	0	0	1.00	1.03	1.23	1.49	0.44	87.36	7.37	12.64
Sand	0	0	0	0	0	0	11.94	0	7.32	85.61	14.39

From the confusion matrix presented in Table 4, we can see that sparse grass and bare land were the most confusing classes, with omission portions accounting for 26.8% and 25.4%, respectively. The classification accuracy of the *Carex* community was 89.3%, which was higher than the *Phragmites* community (87.4%) and *Artemisia* community (81.5%). About 7.4% of the *Phragmites* community was wrongly classified as sand. The *Artemisia* community was often confused with bare land (accounts for 10.5%). Total accuracy of the classification was 84.2% (1,418/1,684), and the Kappa coefficient was 0.81. Assessment of the classification uncertainty indicated that the vegetation information derived from the Landsat 8 remote sensing image was evident in this study.

The area covered by dominant communities in the Poyang Lake wetland was 1,120.12 km^2, accounting for 40.0% of the study area (Figure 5 and Table 5). *Carex* was the most widespread community, with an estimated percentage of 16.3%. The area of the *Phragmites* community was 310.69 km^2 and the area of the *Artemisia* community was 123.71 km^2, accounting for 8.5% and 3.4% of the total area, respectively.

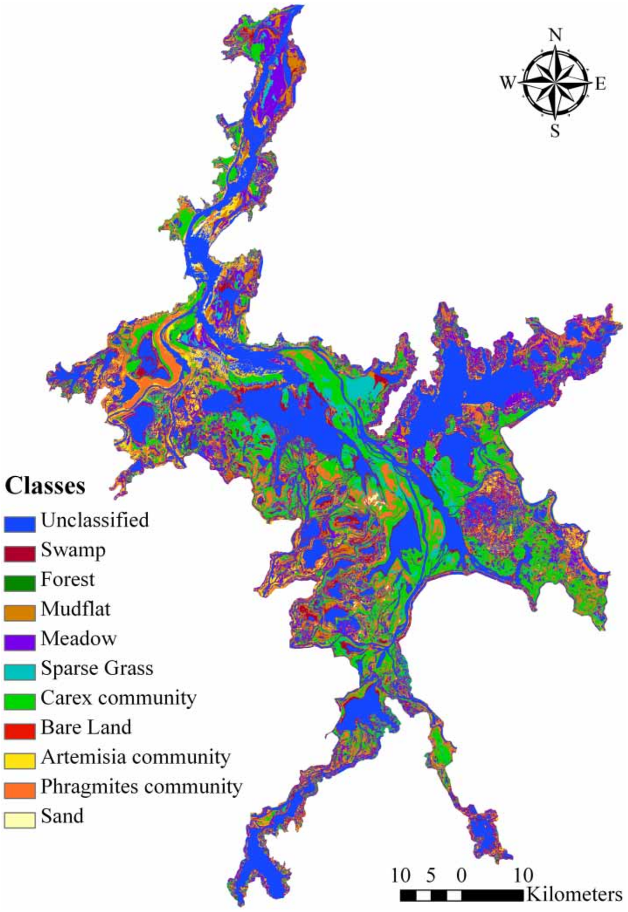

Figure 5 | Classification of a remote sensing image (LC81210402013358LGN00) representing the major wetland cover types. 'Unclassified' coverage corresponds to areas rejected by the threshold of NDVI (not included in wetland classification).

Table 5 | Area and percent coverage of the major cover types in the Poyang Lake wetland

Classes	**Area (km²)**	**Coverage (%)**
Communities		
Carex	591.46	16.4
Phragmites	310.69	8.6
Artemisia	123.71	3.4
Others	94.26	2.6
Meadow	528.89	14.6
Mudflat	307.22	8.5
Sparse grass	218.97	6.1
Swamp	205.13	5.7
Bare land	67.61	1.9
Forest	38.71	1.1
Sand	23.3	0.6
Unclassified	1,107.72	30.6
Total	3,617.67	100.00

With fertile sediments and a relative lack of disturbance by human activity, alluvial plains provide an ideal environment for vegetation growth. Therefore, wetland vegetation communities are mainly distributed on the alluvial plains, such as the PLNNR in Wucheng and the NWNNR in Nanji (Figure 5). The *Carex* community was typically found in the delta front of big rivers and on the flat floodplains of the dish-shaped pit groups. A significant proportion of the *Phragmites* community was distributed along levees and on the higher plains of the dish-shaped pit groups. The *Artemisia* community was usually dispersed along river banks, and always mixed with the *Carex* community and *Phragmites* communities. Due to the complicated distribution and lower classification accuracy of the *Artemisia* community, it is not discussed in the following results.

Water regimes

Outputs from MIKE 21 included nodal water levels, total depth, and the outflow at Hukou. Based on the digital elevation model for the study area, specific water regimes during 2006–2012 (characterized here by IDU, IDE, and IFR) were calculated and averaged, as shown in Figure 6. Annual average IDU and IDE generally varied along the gradient of the elevation, exhibiting maximum values within the deep flow channels and permanently flooded sub-lakes (Figure 6(a) and 6(b)). The distribution of annual average IFR was not consistent with the exact variation of elevation (Figure 6(c)). IFR in the south-branch delta of Ganjiang exhibited more significant spatial heterogeneity due to the complex river networks and the management of the sub-lakes in the southern wetland. The rasterization processes for all of the water regimes were executed by the kriging interpolation method, according to the 30 m spatial resolution of Landsat 8.

Distribution of vegetation in relation to water regimes

Step sizes (intervals) of IDU, IDE, and IFR were specified as 18 days, 0.2 m, and 1 time, respectively. Areas of both typical communities were calculated and fitted by the Gaussian regression model along the gradients of each water regime (Figure 7). The optimal IDU of the *Carex* community (159 days) was found to be longer than the *Phragmites* community (144 days). The *Carex* community (50 days) was able to survive a little longer IDU than the *Phragmites* community (48 days). Figure 7(b) shows an optimal IDE of 0.89 m for the *Carex* community, and 0.78 m for the *Phragmites* community. Amplitude of IDE in the *Carex* community ranged from 0.13 m to 1.68 m, which was wider than the amplitude in the *Phragmites* community (0.18 m–1.38 m). Optimal IFR for the *Phragmites* community and the *Carex* community were both between 2 and 3 times. The *Carex* community tolerates a wider amplitude of IFR than the *Phragmites* community. The fitting results of relative abundance along IFR (mean Adj. $R^2 = 1.00$) were better than IDU (mean Adj. $R^2 = 0.88$) and IDE (mean Adj. $R^2 = 0.83$). However, this does not mean that IFR is the most important determinant of vegetation distribution.

To evaluate the integrated and individual effects of water regimes on community distribution, the average conditions of each water regime and the percentage of each community were calculated along the gradient of elevation within the PLNNR and analyzed by canonical correspondence analysis (CCA), with respect to the water level difference between north and south sections of the lake (Figure 8 and Table 6). The first eigenvalue (0.45) was canonical; the other three were not since there were only two species analyzed in this study. The CCA showed that the percentage of the cumulative variance of the first axis was 81%, accounting for 90% of the information regarding the relationship between species and environments.

In the CCA biplots (Figure 8), all variables were closely related to Axis 1, indicating an obvious water regime gradient along the first axis. A significant specific proportion (89%,

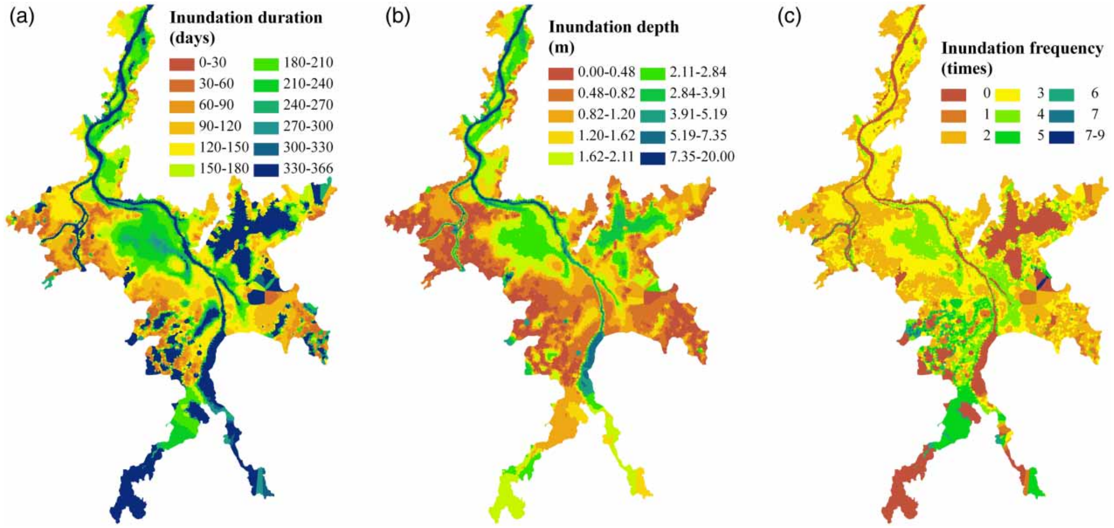

Figure 6 | Spatial distribution of (a) IDU, (b) IDE, and (c) IFR within the Poyang Lake wetland.

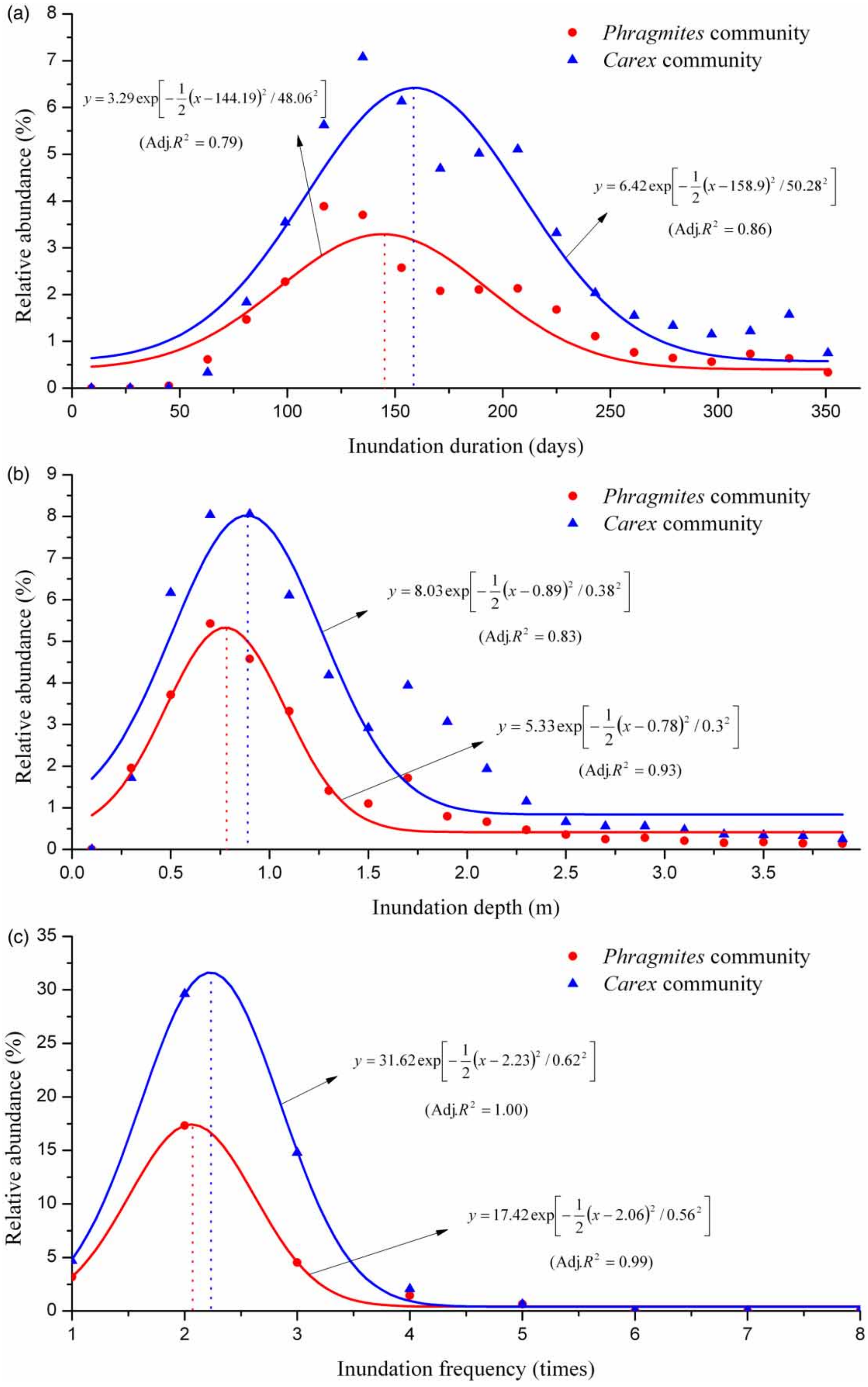

Figure 7 | Distribution of typical vegetation communities along the gradient of (a) IDU, (b) IDE, and (c) IFR. The equation and performance of Gaussian regression are shown in each panel.

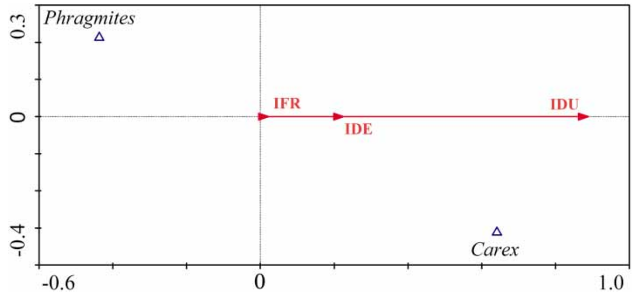

Figure 8 | Biplot of the final CCA showing the distribution of both typical vegetation communities along the gradient of IDU, IDE, and IFR.

Table 6 | Results from the CCA analysis

	SPEC AX1	ENVI AX1	IDU	IDE	IFR
SPEC AX1	1.00				
ENVI AX1	0.90**	1.00			
IDU	0.80**	0.89**	1.00		
IDE	0.20	0.23	0.64**	1.00	
IFR	0.02	0.02	−0.20	−0.33	1.00

Relationship of species axes, environmental axes, and hydrological variables. In turn, each environmental axis can be defined as a combination of the hydrological variables.
**Indicates that slope is significant at the level of 0.01 by T-test.

$p < 0.01$) of the environmental axis could be explained by IDU. Meanwhile, more than 80% of the variance of vegetation composition could be explained by IDU ($p < 0.01$), suggesting a positive correlation between IDU and the richness of the *Carex* community, and a negative correlation between IDU and the richness of the *Phragmites* community. In contrast, IDU was significantly correlated with IDE ($r = 0.64$, $p < 0.01$).

DISCUSSION AND CONCLUSION

This study is among the first to link vegetation distribution and hydrologic conditions at a spatial scale larger than 3,000 km^2. The *Carex* community has been shown to favor more hydric environments with longer IDU and deeper IDE, compared with the *Phragmites* community. The differences in hydrological preferences between the two major communities observed in this study were consistent with previous studies (Hu *et al.* 2010; Sang *et al.* 2014; Xu *et al.* 2015). We know that fluctuations in water level affect plant establishment from the seed bank by stimulating or inhibiting germination, modifying oxygen availability in the soil (and the subsequent concentrations of nutrients and toxic substances), desiccating aquatic plants or inundating terrestrial plants, and changing light availability with changes in depth (Mitchell & Rogers 1985). IDU and IDE affect the distribution of individual communities due to species tolerance of anoxia, as low oxygen availability reduces respiration and growth in nonadapted roots and can eventually lead to the death of root meristems (Laan *et al.* 1991; Van den Brink *et al.* 1995). Under these conditions, some microorganisms use electron acceptors other than oxygen for respiration, resulting in the formation of potentially phytotoxic metal ions such as Fe^{2+} (Laan *et al.* 1989) and Mn^{2+} (Waldren *et al.* 1987). Moreover, the accumulation of harmful gases, such as ethylene, can also damage plant organs or at least limit plant growth (Visser *et al.* 1997). Additionally, IFR can affect species richness when an intermediate frequency creates establishment opportunities for species and prevents competitive exclusion (Bornette *et al.* 1994) consistent with the intermediate disturbance hypothesis (Connell 1978).

For the three factors examined by CCA, IDU alone had a significant effect on the distribution of plant communities. In contrast, IDE and IFR were less important in this study. Anoxic conditions may develop once a site is inundated. These conditions vary little with depth, and may gain additional discriminatory power. Furthermore, due to the low slope of the delta in the Poyang Lake wetland, slight changes in elevation can play large roles in the influence of IDE on vegetation distribution. The frequency of flood disturbances within grasslands varies in a narrow range (generally 1 to 3 times), under the influence of the subtropical monsoon. This may partially contribute to the limited correspondence between community composition and IFR. Researchers have diverged in their assessments of individual water regimes. For instance, Zweig & Kitchens (2009) showed that IDE was the primary mechanism in driving vegetation community change in the Everglades ecosystem. In contrast, Huang *et al.* (2013) found that IDE and IFR were not as important as the IDU of flooding. It is noteworthy that water transparency played a key role in the action of IDE. Studies have shown that vegetation types also affect the performance of individual water regimes. Additionally, environmental stresses and human-caused disturbances that may be occurring at multiple scales often obscure or alter the relationships of individual species or communities to hydrologic conditions (Schueler 1994; Gwin *et al.* 1999).

IDU, IDE, and IFR all affected the distribution of plant communities in certain ways, although for the PLNNR, only IDU was significant when the individual effect of water regimes was examined by CCA. IDU was highly correlated with IDE in this study. However, IFR is usually closely linked with IDE and IDU (high frequency of short shallow floods versus frequency of long deep floods) and thus the effects of IFR can be difficult to isolate (Casanova & Brock 2000). The distribution of plant communities under natural, fluctuating water regimes is a consequence of hydrology changes and their interactions with a suite of other variables, including: nutrients, soil characteristics, competition among species, pathogen activity, fire regimes, and biota (Zweig & Kitchens 2008).

Human activities, especially the construction of TGD, have made the Poyang Lake wetland drier in the 21st century. The proposal for a Poyang Lake Project (PLP, a control structure at the Lake outlet to manage dry season discharge) could provide an effective way to balance the operation of the TGD in the upper Yangtze River and water storage in Poyang Lake (Wang *et al.* 2015). Operation of PLP will undoubtedly change the water level fluctuations and hydrological processes of the lake, and subsequently affect wetland vegetation, water quality, and the migration of aquatic species. For instance, the operation of PLP will raise the water level of Poyang Lake in the dry season. Sustained high water levels will increase the depth and duration of inundation over the wetlands. As a result, longer IDU and deeper IDE may lead to the degradation of floating and submerged vegetation at lower elevations, and the succession of emergent aquatic vegetation to mesophytic and semi-aquatic vegetation at higher elevations. The hydrological preferences of the two major vegetation communities indicated in this study provide a series of practical references for the management of hydro-engineering projects.

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