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Unnatural flooding alters the functional diversity of riparian vegetation of the Three Gorges Reservoir

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Abstract

1. The response of riparian vegetation to flow regulation has been a research focus for decades. Several studies have shed light on the effects of flow stabilisation on riparian woody species, but other life forms exposed to intensified inundation have been overlooked. Furthermore, studies from a functional perspective are scarce.
2. We evaluated the functional response of riparian vegetation along the shores of the Three Gorges Reservoir on the Yangtze River in China to unnaturally long annual flooding (>7 months) after the first year of filling. We aimed to answer the following: (1) can we derive well-defined flow-response guilds from the riparian zones of the Yangtze River? and (2) which plant traits and guilds are favoured or disfavoured by the unnaturally long flooding environment?
3. Woody and herbaceous species were inventoried in 12 reaches along the shorelines of the Three Gorges Reservoir and another 12 reaches along the free-flowing Yangtze River. We performed a cluster analysis to derive riparian guilds using abundance data (projective coverage) from 40 riparian plant species and 13 responsive traits. Structural composition and functional diversity of the unnaturally and naturally flooded riparian vegetation were compared.
4. Unnaturally long flooding substantially reduced species richness, but it did not change the riparian vegetation cover. This novel flooding reduced functional diversity, mostly owing to the loss of stress-tolerant woody species and competitive perennial herbs. However, competitive annual herbs and flood-tolerant riparian herbs, as the most abundant functional guilds, were favoured even under such long-term hypoxic conditions.
5. These guilds under regulation revealed a high functional resilience to prolonged flooding along the upstream reaches of the Yangtze River. Flooding tolerance and the capacity to synchronise germination and growth with short-exposure periods underlie the plant species changes. Our findings are useful for anticipating the effects of long-lasting inundation on riparian areas triggered by flow regulation or warmer climates. The functional perspective lends confidence that our conclusions can be generalised to other geographical regions despite not sharing the same species pool. Finally, the plant species that showed a high flooding tolerance should be considered for the restoration of riparian areas affected by the Three Gorges Reservoir.

KEYWORDS
flow regulation, impoundment, plant trait, riparian zone, river

1 | INTRODUCTION

Many of the world's rivers are regulated by dams (>15 m high) for various purposes (Grill et al., 2019). Flow regulation, however, has many adverse effects on river ecosystems (Nilsson, Reidy, Dynesius, & Revenga, 2005), such as resettlement (Gillett & Tobias, 2002), obstruction of dispersal and migration of organisms (Merritt & Wohl, 2006), modification of aquatic and riparian communities (Gehrke, Gilligan, & Barwick, 2002; Tockner & Stanford, 2002), and alteration of downstream sedimentation patterns and seasonal variation in water temperature (Poff et al., 1997). Thousands of large dams are under construction or being planned, especially in Asia, Africa, and South America (Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). Among these regions, the Yangtze River Basin in China has experienced the most intensive dam construction (Zarfl et al., 2015).

The global boom in dam building is mainly motivated by an increased demand for hydropower, which contributes 80% to clean energy (The World Bank, 2014). Besides providing energy, dams also play a key role in mitigating increased flood risk worldwide triggered by a warmer climate (Hirabayashi et al., 2013). The Three Gorges Dam (TGD) and its Reservoir (TGR) on the Yangtze River provide an excellent model of integrating these functions. To reduce downstream flood hazards, the TGR reserves capacity during the rainy season by maintaining a low-water level and gradually raises the water level for hydropower production during the other seasons (Su et al., 2013). Under this operation mode, riparian vegetation along some upstream reaches of the TGR is subject to an unnaturally long annual flooding resulting from the combination of natural seasonal floods and artificial inundation (Su et al., 2013). The response of riparian vegetation to such long-term hypoxic conditions is less documented.

Riparian vegetation has important functions for adjacent terrestrial and aquatic ecosystems, such as enhancing regional biodiversity (Sabo et al., 2005), producing organic matter (Tockner & Stanford, 2002), driving nutrient cycling, purifying water, and supplying habitats for animals (Capon et al., 2013; Kominoski et al., 2013). Recently, the functional responses of riparian vegetation to flow alterations have been a focus of research. Such studies have aimed to understand the linkages between anthropogenic disturbance and ecosystem functions and processes under the assumption that the functional approach allows generalisations and comparisons among different fluvial systems (Merritt, Scott, Poff, Auble, & Lytle, 2010). Moreover, evaluating the resistance, resilience, and sensitivity of riparian vegetation to flow management may ultimately rely on this functional approach (Walker, Kinzig, & Langridge, 1999). This approach was successfully applied to elucidate the adaptive strategies of riparian plants to fluvial disturbance (Aguiar et al., 2018; Bejarano, Nilsson, & Aguiar, 2018; Stromberg & Merritt, 2016). Bruno, Gutiérrez-Cánovas, Sánchez-Fernández, Velasco, and Nilsson (2016) and Lozanovska, Ferreira, and Aguiar (2018) quantified these functional changes using functional indices. However, most of these studies exclusively analysed woody species along the downstream-from-the-dam riparian areas, overlooking the responses of herbs upstream from the dam. This might have been due to the difficulties in developing comprehensive trait databases for many herbaceous species and the absence of dam-controlled upstream riparian areas in relatively small reservoirs studied. However, effects on the vegetation upstream are as significant as those on the vegetation downstream for large reservoirs such as the TGR. A thorough understanding of the functional responses of the riparian vegetation including different life forms to flow-regulation scenarios occurring upstream of large reservoirs is required.

To address this research gap, we compared, from structural and functional perspectives, the species richness and abundance, guild richness, species redundancy, and functional diversity, of the riparian vegetation both under and outside the control of the TGR. We randomly selected 12 reaches along the shorelines of the TGR subjected to natural and artificial long-term annual flooding and another 12 reaches along the free-flowing Yangtze River. Fieldwork was conducted in the first year after the filling of the TGR to explore the functional response of riparian woody and herbaceous species to the new flooding conditions. We aimed to answer the following questions: (1) can we derive well-defined flow-response guilds from the riparian zones of the regulated and free-flowing Yangtze River? and (2) which plant traits and guilds are favoured or disfavoured by the new inundated environment? Accordingly, we hypothesised that (1) it is likely to derive riparian plant guilds that possess distinct suites of responsive traits; and (2) the species richness, redundancy of all plant guilds, and overall functional diversity of riparian vegetation along the regulated reaches would be lower than those of the free-flowing reaches. The underlying reasoning for these hypotheses derives from the understanding that the unnaturally long flooding leads to extremely long hypoxic conditions and short-exposure periods that disfavour the survival and recruitment of those riparian plants that are unable to deal with such conditions.

2 | METHODS

2.1 | Study area

The TGD lies on the Yangtze River in South–Central China and regulates 660 km of upstream water along the main stem to Jiangjin City (Figure 1). The total area of the reservoir region (106°–111°50′E, 29°16′–31°25′N) is 58,000 km^2 (Wu et al., 2004), with a humid, subtropical monsoonal climate; mean annual temperature ranging between 15 and 19°C; and mean annual precipitation of 1,250 mm (Wu et al., 2004). The annual peak flow of the Yangtze River occurs during the rainy season from June to September (Figure 1).

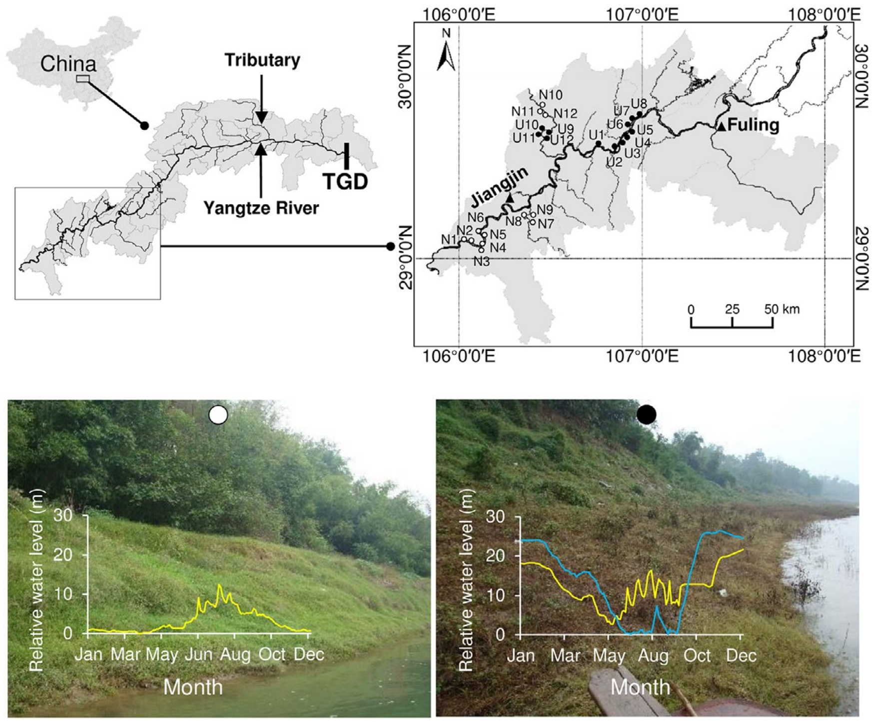

FIGURE 1 Map of the Three Gorges Reservoir region showing the locations of the study sites (upper panel). Black lines indicate the Yangtze River and its tributaries controlled by the Three Gorges Dam (TGD). Empty circles and filled circles represent the sites of naturally and unnaturally flooded riparian zones (NFRZ and UFRZ, abbreviated as N and U), respectively. The water level regimes of the NFRZ (left-lower panel), UFRZ, and Three Gorges Reservoir (yellow and blue lines, respectively; right-lower panel) in 2009 are shown. Relative water level is the vertical distance from the historically lowest water level of the studied reaches. See Table S1 for coding and more information of the study sites

TABLE 1 Comparison of the environmental factors between the naturally flooded riparian zone (NFRZ) along the Yangtze River and the unnaturally flooded riparian zone (UFRZ) regulated by the Three Gorges Reservoir

Environmental variables	NFRZ (*n* = 12)	UFRZ (*n* = 12)	*p*
Height of riparian zone (m)	9.5 ± 0.26	8.3 ± 0.71	0.146
Slope (degree)	18.3 ± 0.94	15.8 ± 0.85	0.062
Substrate diversity	3.6 ± 0.31	3.1 ± 0.29	0.252
Substrate fineness	0.2 ± 0.71	0.8 ± 0.68	0.506
Submergence duration (d)	44 ± 0.7	214 ± 10.9	**<0.001**
Daily discharge (m^3/s)	4,360.4 ± 1,016.96	7,606.1 ± 1,180.46	**0.049**

Note: Values are mean ± 1SE. Student *t*-tests were applied. *p* values at the 95% confidence level are in bold

The operation of the TGD has the following three goals: an improvement in the commercial navigation along its upstream reaches, reduction in flood risk downstream from the reservoir, and production of electric power (Changjiang Water Resource Commission, 1997). To enlarge the waterway, managers raised the water level of the Yangtze River upstream from the TGD from 68 to 145 m above sea level (a.s.l.) in the dam site. To mitigate downstream flood hazards during the rainy season, the reservoir must accommodate upstream peak flows by maintaining the impoundment water level at 145 m a.s.l. (Figure 1). For hydropower production, the water level was progressively raised to 175 m a.s.l. from September to December, maintained at that level until February the subsequent year, and gradually returned to 145 m a.s.l. by the end of May (Su et al., 2013; Figure 1). These artificial annual fluctuations resulted in several hundred kilometres of backwater area between the dam and Jiangjin City in the main stem and tributaries upstream from the TGD. In particular, the riparian zone of the Yangtze River and tributaries between Fuling and Jiangjin Cities naturally flood in summer when the TGD operates at a low-water level, and after the rainy season, the riparian zone submerges again in autumn and winter when the TGD operates at a high-water level. Consequently, the riparian zone in this area experiences >7 months of flooding due to the combination of seasonal flooding and reservoir-induced inundation (Figure 1; Table 1).

2.2 | Data collection

2.2.1 | Study sites

To explore the responses of riparian vegetation to unnaturally long annual flooding, fieldwork was conducted in 2009, the first year after the filling of the TGR. To sample various types of riparian vegetation, 12 sites were randomly selected in the main stem section between Fuling and Jiangjin Cities and a tributary of the Yangtze River where both natural and artificial flooding of the riparian zone occurs (Figure 1; Table S1). Another 12 reference sites were randomly selected in the main stem section upstream of Jiangjin City and two tributaries of the Yangtze River where flooding of the riparian zone occurs only in rainy season (Figure 1; Table S1). The riparian zones of all study sites were not disturbed by any other human activities except the water flow of the TGR.

2.2.2 | Vegetation investigation and plant trait selection

To ensure that the two types of riparian zone were comparable, we investigated them in September, just before the rise in the water level in the TGR. At this time of the year, the vegetation in the naturally and unnaturally flooded riparian zones (NFRZ and UFRZ, respectively) was exposed and maximally recovered from the preceding flood, which occurred in the summer in the NFRZ and in the summer, autumn, and winter in the UFRZ. Each site comprised a 130-m-long stretch of riverbank. The NFRZ referred to the area between the winter low-water and summer high-water levels (Figure 1), and the UFRZ was identical to the area between the spring low-water and winter high-water levels. To encounter most species, we sampled 30 plots, 2 × 2 m in size, 10 m apart along low, intermediate, and high elevations in each site (10 plots per elevation). All plant species were inventoried except for mosses and lichens, which were scarce. For each species in a plot, we measured the average height of 10 randomly selected individuals and recorded the abundance by estimating the projective canopy coverage.

Thirteen functional traits (Table S2), including morphological, phenological, reproductive, and ecological traits of 40 woody and herbaceous species whose coverage exceeded 2% across all plots in each site were selected. The categorical traits were obtained from the *Flora Reipublicae Popularis Sinicae* (http://www.iplant.cn/frps) and field observations, and the numerical traits were extracted from databases and publications (Tables S3 and S4). We averaged the values of the numerical traits, which were from multiple sources. Fieldwork and measurements were carried out following the protocol of Cornelissen et al. (2003) when the above data sources were not available.

2.2.3 | Environmental variables

In each site, we measured the slope and height of the riparian zone, namely the vertical distance between the lowest and highest water levels, using an altimeter (E203, 1 m accuracy; Suunto Oy, Vantaa, Finland). We inventoried the number of substrates in each site following the Wentworth's particle size classification, which classified the substrate into six categories, namely, clay, silt, sand, gravel, boulder, and bedrock (Wentworth, 1922). We visually estimated the coverage of each substrate type in every plot and calculated the substrate fineness using the following equation:

$$\text{Substrate fineness} = \sum_{i=1}^{X} (Ci \times Vi)$$

where, C_i is the coverage of substrate *i*, V_i is the assigned Chorley's value of substrate *i* (Chorley, 1984), and *X* is the number of substrate types. For each site, the submergence duration was calculated by averaging the submergence duration of three elevations. We used the mean daily discharge throughout the year, which was downloaded from the nearby gauging stations (http://xxfb.hydroinfo.gov.cn/).

2.3 | Data analysis

2.3.1 | Environment

To determine the environmental similarity between the UFRZ and NFRZ, we compared the height, slope, substrate diversity, substrate fineness, submergence duration, and mean daily discharge between the sites from UFRZ and NFRZ using Student *t*-test ($n = 12$).

2.3.2 | Species diversity

The recorded plant species were grouped according to their morphology (i.e. trees + shrubs, forbs + ferns, and graminoids) and life history (i.e. annuals + biennials and perennials). In each site, we recorded the total number of species (all plant species found in each site), number of species of different morphologies and life histories. The averaged total cover (summed projective cover of all species in each plot) and averaged percentage cover for different species groups (projective cover of each group divided by the total cover) of 30 plots in each site were calculated. The species richness, species richness of different morphology and life history groups, and total cover and percentage cover of each group were compared between the sites from UFRZ and NFRZ using Student *t*-test ($n = 12$). The dissimilarity in species composition (presence and absence) between the sites from UFRZ and NFRZ was tested using the analysis of similarities (ANOSIM; a non-parametric statistical test of significant differences; Clarke, 1993) and was visualised using non-multidimensional scaling analysis (an indirect gradient analysis; Shepard, 1962) based on Bray–Curtis distance.

2.3.3 | Classification of guilds

To obtain riparian guilds, we applied a hierarchical classification of species using a functional trait matrix (species and traits) derived from the Gower distance (which allows measurements between entities characterised by categorical and numerical values; Gower, 1971), and the unweighted pair group average method. We validated the obtained groups (i.e. riparian guilds) based on significance ($p < 0.05$) and the degree of segregation in the ANOSIM tests ($R < 0.25$ denotes no separation between groups, values between 0.25 and 0.50 denote some overlap, values between 0.5 and 0.75 indicate slight overlap, and $R > 0.75$ indicates well-segregated groups). Values of functional traits were averaged for each guild, and the most distinctive traits in relation to the remaining guilds were used to name the guilds. A principal coordinate analysis (PCoA), based on Gower distance, was performed to better visualise the relationships between guilds and traits.

2.3.4 | Functional diversity

The number of guilds and species redundancy for each guild between UFRZ and NFRZ were compared using the non-parametric Wilcoxon rank-sum test (n = 12). Species redundancy was calculated as within-guild recorded number of species per site relative to the total number of species of that guild based on hierarchical classification (Bejarano et al., 2018). We determined guild abundance in each site by the summed abundance of species belonging to a guild recorded in each site and compared abundance between UFRZ and NFRZ using the Wilcoxon rank-sum test (n = 12). We used functional richness (FRic) and functional dispersion (FDis; see Kuebbing, Maynard, & Bradford, 2018), both of which are the most frequently applied in cases of flow regulation, land use, and species invasions (Lozanovska et al., 2018), to reflect functional diversity changes in UFRZ and NFRZ. A generalised linear model (GLM) and Student t-test were applied, respectively, to compare the FRic and FDis between UFRZ and NFRZ (n = 12). The GLM was applied because the data violated the assumption of normal distribution. We performed all analyses using R statistical package (R Core Team, 2015), packages stats (R Core Team, 2015; t.test function for Student t-test and wilcox.test function for Wilcoxon rank-sum test), vegan (Oksanen et al., 2018; metaMDS and anosim functions for non-multidimensional scaling analysis and ANOSIM, respectively, hclust function for clustering analysis, and cmdscale function for PCoA), and FD (Laliberté, Legendre, & Shipley, 2014; dbFD function for calculating functional diversity metrics).

3 | RESULTS

3.1 | Environment

No difference was observed among the environmental factors characterising the UFRZ and NFRZ (Table 1, Student t-test, $p > 0.05$), except that UFRZ was exposed to considerably longer submergence ($p < 0.001$) and higher discharge ($p = 0.049$) than NFRZ.

3.2 | Species diversity

Both total species richness and species richness of different groups were lower in the UFRZ (Figure 2a). The total species richness in UFRZ was 59.3% lower than that in NFRZ (Student t-test, $p < 0.001$). The number of woody species, forbs and ferns, and graminoids in UFRZ was 71.2% ($p < 0.001$), 60.1% ($p = 0.001$), and 55.0% ($p < 0.001$) lower than that in NFRZ, respectively. Similarly, the number of annuals + biennials and perennials in UFRZ was 59.1% ($p = 0.014$) and 61.8% ($p < 0.001$) lower than that in NFRZ, respectively. The total cover of riparian vegetation and the percentage cover of all species groups did not change (Figure 2b, Student t-test, $p = 0.072$ for total cover, $p = 0.125$, $p = 0.634$, $p = 0.177$, and $p = 0.177$ for forbs and ferns, graminoids, annuals + biennials, and perennials, respectively), except for the percentage cover of trees and shrubs in the UFRZ, which was lower than that in the NFRZ ($p < 0.001$). The species composition of riparian vegetation significantly changed in the UFRZ compared with that in the NFRZ (Figure 3, ANOSIM, $R_{ANOSIM} = 0.494$, $p = 0.001$).

3.3 | Functional diversity

Out of the 40 plant species in the UFRZ and NFRZ, six riparian guilds were identified based on the classification analysis (Table 2; Figure 4, Global $R_{ANOSIM} = 0.865$, $p = 0.001$), including competitive annual herbs (e.g. *Polygonum hydropiper* and *Xanthium sibiricum*), competitive

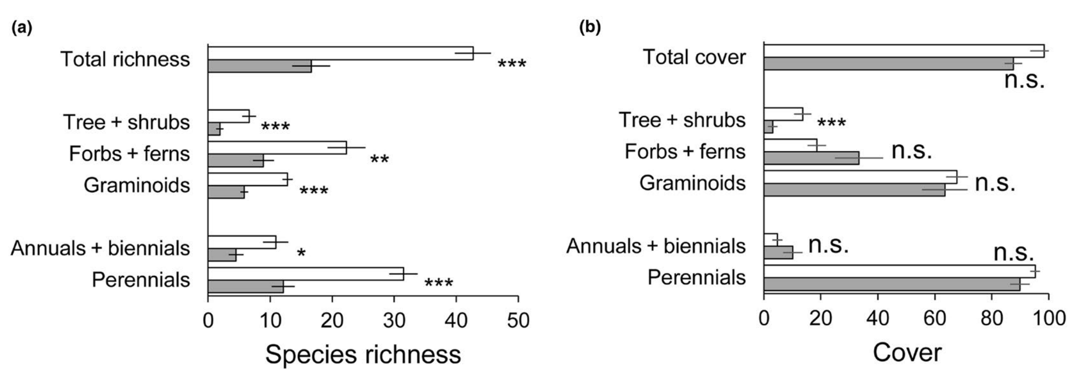

FIGURE 2 Comparison of (a) the total species richness and richness of different species groups, and (b) the total cover and percentage cover of different species groups between naturally and unnaturally flooded riparian zones (white and grey bars, respectively). Values are mean ± 1*SE* (n = 12). Student t-test was applied. *, **, and *** mean that significant differences were observed at the 95, 99, and 99.9% confidence levels, respectively; n.s. indicates that no difference was observed at the 95% confidence level

perennial herbs (e.g. *Eupatorium adenophora* and *Imperata cylindrica*), stress-tolerant herbs (e.g. *Arthraxon hispidus*), flood-tolerant riparian herbs (e.g. *Cynodon dactylon*, *Hemarthria altissima*, and *Phragmites karka*), competitive woody species (e.g. *Morus alba* and *Pterocarya stenoptera*), and stress-tolerant woody species (*Ficus tikoua*). All guilds were well segregated (all paired $R_{ANOSIM} > 0.75$). The first two most important dimensions for the PCoA explained 66.7% of the variation (Fig. S1).

The UFRZ had fewer guilds than the NFRZ (Table 3, Wilcoxon rank-sum test, $p < 0.001$), and 73.9% of this variation was explained by the absence of stress-tolerant woody species and competitive

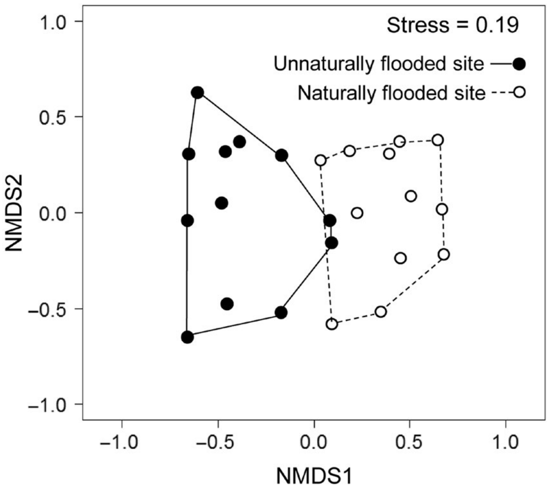

FIGURE 3 Non-multidimensional scaling (NMDS) ordination of all study sites. Each point represents the plant species composition of a naturally or unnaturally flooded riparian site. Points closer to each other are more similar in terms of species composition. The extent of the range in variation for each type of site is delineated with different line types and shades that match the shade of the points

perennial herbs (not shown in Table 3). The FRic of the UFRZ was lower than that of the NFRZ (GLM, $p = 0.001$); however, the FDis of the UFRZ did not significantly differ from that of the NFRZ (Student *t*-test, $p = 0.050$). The species redundancy of competitive annual herbs was higher in the UFRZ than in the NFRZ (Figure 5a, Wilcoxon rank-sum test, $p = 0.027$). However, the species redundancy of stress-tolerant woody species and competitive perennial herbs was lower in the UFRZ than in the NFRZ ($p = 0.001$). The species redundancy of competitive woody species, stress-tolerant herbs, and flood-tolerant riparian herbs in the UFRZ did not differ from those in the NFRZ ($p = 0.075$, $p = 0.149$, and $p = 0.999$, respectively). The abundance of competitive annual herbs and flood-tolerant riparian herbs was higher in the UFRZ than in the NFRZ (Figure 5b, Wilcoxon rank-sum test, $p = 0.034$ and $p = 0.005$, respectively). However, the abundance of stress-tolerant woody species and competitive perennial herbs was lower in the UFRZ than in the NFRZ ($p < 0.001$ and $p = 0.002$, respectively). No difference was observed in the abundance of competitive woody species and stress-tolerant herbs between the two types of riparian areas ($p = 0.209$ and $p = 0.071$, respectively).

4 | DISCUSSION

The response of riparian vegetation guilds to flow changes has been well documented in recent studies involving flood stabilisation and water abstraction along downstream reaches from dams (see Aguiar et al., 2018; Bejarano et al., 2012; Bruno et al., 2016; Stromberg & Merritt, 2016). Nevertheless, riverine herbaceous species representing much of the biomass in riparian communities and being considerably more sensitive to stream flow than woody species have been

TABLE 2 Description of six guilds derived from 40 species based on 13 functional traits

Guilds	Description	Species
G1: Competitive annual herbs	Tall annual herbs, fast growing, large canopy, light demanding, mostly distributed in the middle or/and high elevations of the riparian zone	*Mosla scabra*, *Perilla frutescens*, *Polygonum hydropiper*, *Urena lobate*, *Xanthium sibiricum* (5 species)
G2: Competitive woody species	Mostly are deciduous trees and shrubs, 2 to 30 meters high, light demanding, distributed in middle or high elevations of riparian zone	*Campylotropis macrocarpa*, *Erythrina variegata*, *Morus alba*, *Populus simonii*, *Pterocarya stenoptera*, *Robinia pseudoacacia*, *Salix variegata (evergreen)*, *Swida paucinervis*, *Vitex negundo* (9 species)
G3: Stress-tolerant woody species	Prostrated woody species, middle or low light demanding, usually growing under canopy	*Ficus tikoua* (1 species)
G4: Stress-tolerant herbs	Short, small canopy, slow growing, middle or low light demanding, usually growing under canopy	*Arthraxon hispidus*, *Gonostegia hirta*, *Justicia procumbens* (3 species)
G5: Competitive perennial herbs	Tall, fast growing, large canopy, mostly light demanding or half-light demanding	*Cyclosorus aridus*, *Deyeuxia arundinacea*, *Dichanthium annulatum*, *Eupatorium adenophora*, *Humulus japonica*, *Imperata cylindrical*, *Neosinocalamus affinis*, *Pteris vittata*, *Saccharum arundinaceum* (9 species)
G6: Flood-tolerant riparian herbs	Clonal and flood-tolerant herbs, mostly graminoids, found only in riparian zone or wetlands in the study area, high resprouting ability, distributed in middle or low elevations of riparian zone	*Alternanthera philoxeroides*, *Arundinella anomala*, *Carex heterostachya*, *Cynodon dactylon*, *Cyperus rotundus*, *Equisetum ramosissimum*, *Hemarthria altissima*, *Paspalum paspaloides*, *Phalaris arundinacea*, *Phragmites karka*, *Polygonum chinense*, *Pycreus flavidus*, *Saccharum spontaneum* (13 species)

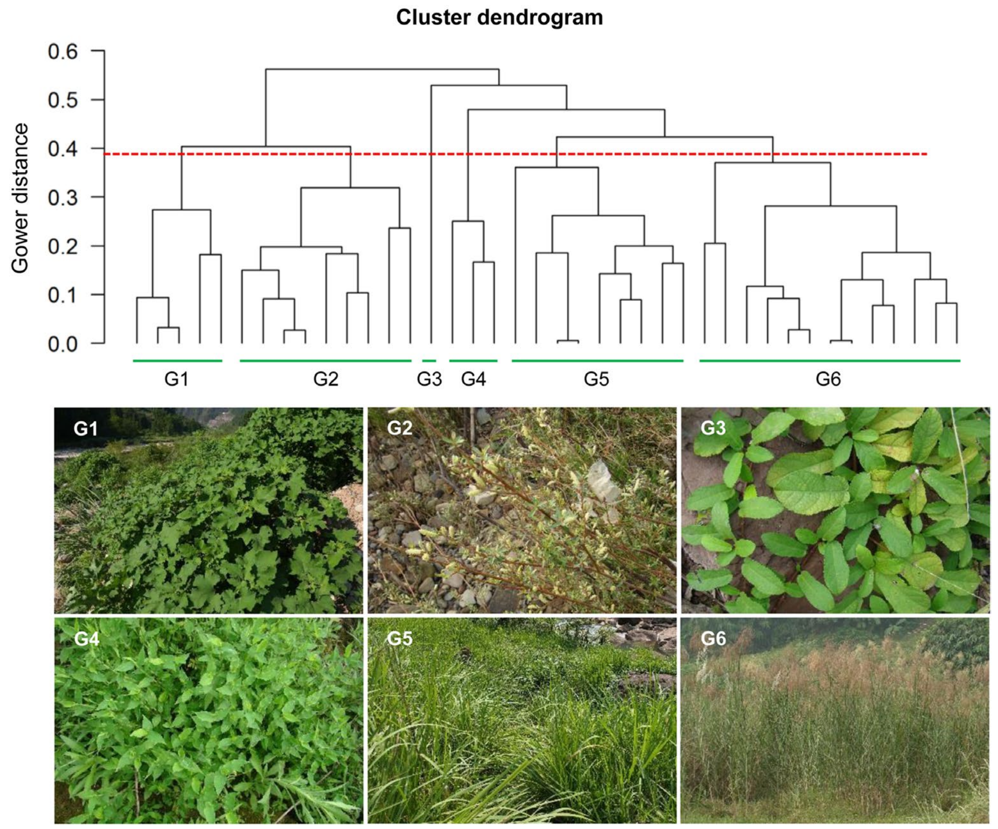

FIGURE 4 Cluster dendrogram of 40 species in naturally and unnaturally flooded riparian zones based on 13 functional traits. The *R* of all paired ANOSIM analyses exceeded 0.75, indicating that well-segregated guilds were derived. Species names for each guild photo: G1, *Xanthium sibiricum*; G2, *Salix variegata*; G3, *Ficus tikoua*; G4, *Arthraxon hispidus*; G5, *Deyeuxia arundinacea*; G6, *Phragmites karka*

TABLE 3 Comparison of functional diversity between naturally and unnaturally flooded riparian zones (NFRZ and UFRZ, respectively)

Functional diversity	NFRZ (*n* = 12)	UFRZ (*n* = 12)	*P*
Guild richness	3.6 ± 0.26	2.2 ± 0.17	**<0.001**[a]
Functional richness (FRic)	0.030 ± 0.006	0.009 ± 0.003	**0.001**[b]
Functional dispersion (FDis)	0.222 ± 0.015	0.176 ± 0.023	0.050[c]

Note: Values are mean ± 1SE. Wilcoxon rank-sum test (a), generalised linear model (b), and Student *t*-test (c) was applied. *p* values at the 95% confidence level are in bold.

omitted from previous functional research. Moreover, despite there being abundant literature on how particular plant species deal with prolonged submergence (e.g. Voesenek, Colmer, Pierik, Millenaar, & Peeters, 2006), there are gaps in our understanding regarding functional approaches to this specific flow scenario. Prolonged inundation characterises the shorelines along large impoundments. Moreover, we envisage future flooding in parts of the currently exposed riverine habitats due to global warming across large areas of South Asia, Southeast Asia, Northeast Eurasia, eastern and low-latitude Africa, and South America (Hirabayashi et al., 2013).

Our findings provide information on the pathways of riverine communities suffering from almost three-times longer inundation than usual, involving persistent hypoxic conditions and frequent fluvial disturbances, limiting both germination and establishment (Bejarano, Sordo-Ward, Alonso, Jansson, & Nilsson, 2020). The guild approach helps develop general frameworks to predict vegetation responses to changing environmental conditions. The observed riparian guild responses to changing flows in the Yangtze River might hopefully be transferred to rivers with little or no existing information in other regions regardless of whether or not they share species.

Six well-defined flow-response guilds were found in the studied locations along the Yangtze River. Despite there being fewer plant species and guilds on the shorelines of the TGR than the natural areas, the most abundant and functional guilds were observed in all locations, which might indicate that the system is highly resilient to disturbance (Mori, Furukawa, & Sasaki, 2013). Most of the removed species belonged to the stress-tolerant woody species guild and the competitive perennial herb guild. The only species from the former guild (*Ficus tikoua*) is likely to disappear due to dam-induced inundation, along with its species-specific pollinator *Ceratosolen* sp. (Zhao, Compton, Yang, Wang, & Chen, 2014). This species has short, prostrated stems that confer a disadvantage when submerged, hindering oxygenation (Voesenek & Blom, 1999). However, no significant consequences are anticipated from the potential loss of this guild, which is very rare in riparian

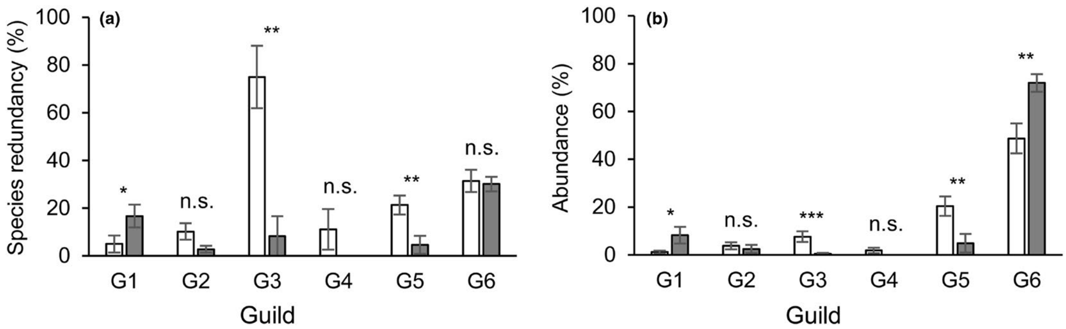

FIGURE 5 Comparison of (a) species redundancy and (b) abundance of each guild between naturally and unnaturally flooded riparian zones (white and grey bars, respectively). Values are mean ± 1*SE* (n = 12). Wilcoxon rank-sum tests were applied. *, **, and *** denote significant differences at the 95, 99, and 99.9% confidence levels, respectively; n.s. indicates that no difference was found at the 95% confidence level. See Table 2 for guild descriptions

areas but abundant in the adjacent uplands. In contrast, the other woody species guild, the competitive woody species guild, was found in the most regulated and natural sites showing a high resilience to unnaturally long flooding owing to species traits, such as tall canopy and high underwater photosynthetic rate, that help to withstand months of flooding (Li, Wei, Geng, & Schneider, 2010; Luo, Zeng, Ye, Chen, & Liu, 2008).

Herbs dominate the upstream reaches of the Yangtze River, and the woody plants are relegated to the background. This substantially differs from other studied regions, such as the semi-arid, Mediterranean, and boreal regions, where woody vegetation is a dominant part of the riparian zone (see Aguiar et al., 2018; Bejerano et al., 2018; Bruno et al., 2016; Stromberg & Merritt, 2016). The competitive perennial herb guild was disfavoured the most by the unnaturally long flooding conditions. Most of the species belonging to this guild are fast growing, competitive, and relatively intolerant to floods, and colonise the boundary towards the uplands (Otsamo, 2000; Peet, Watkinson, Bell, & Sharma, 1999). The decline in this guild may open up a habitat for better-equipped guilds, such as the flood-tolerant riparian herbs and competitive annual herbs. The flood-tolerant riparian herbs exhibited various strategies to cope with oxygen and energy deficiencies under prolonged overhead flooding; example, by retaining relatively high levels of underwater photosynthesis (Luo et al., 2008), absorbing oxygen from the water through many adventitious roots (Ayi et al., 2016), or allocating more nutrients to the roots to reduce the risk of losing carbohydrates (Yao, Zeng, Du, Pan, & Su, 2015). Furthermore, most of these clonal species can quickly re-sprout following submergence, which allows them to take advantage of the short-exposure period before the reservoir is filled again.

These particular traits explain the success of the flood-tolerant riparian herb guild, whose coverage significantly increased under the unnaturally long flooding conditions. As the most abundant guild, the corresponding species provide many key functions in the riparian zone. For example, they are important allochthonous sources of aquatic food for local fish (Li, Xu, Wang, Yue, & Zhang, 2013). Their dense canopy and well-developed root systems provide shelter for animals, regulate geomorphic processes (Arbeiter & Franke, 2018; Xu, Lei, & Zeng, 2017; Xu, Zeng, Lei, & Su, 2011), and increase the activity of soil enzymes and microbial biomass (Ren, Song, Yuan, Ni, & Li, 2018). Consequently, the survival and expansion of this functional guild would be likely to maintain the essential functions of riparian vegetation along the Yangtze River and minimise the encroachment of invasive species.

Opportunists, such as the competitive annual herbs in our study, favoured by stabilised flooding in Mediterranean and semi-arid regions (Aguiar et al., 2018; Stromberg & Merritt, 2016), also thrived under intensified inundation. The dispersal and establishment of these species rely on fluvial disturbance, and dam-induced flooding is likely to promote their dispersal by increasing longitudinal and lateral connectivity. Their establishment, however, must be further filtered by the flooding tolerance of seeds and germination timing (see Lin, Liu, Zeng, Pan, & Su, 2016; Liu et al., 2017). In contrast, herbs with stress-tolerant traits, such as a low light demand and slow growth, were not favoured by the unnaturally long flooding conditions.

In summary, our results indicate a shift in riverine communities towards traits that confer flooding tolerance and rapid and synchronised (with short-exposure period) establishment of species. Conversely, traits related to water-stress tolerance, such as rooting depth, were revealed to be irrelevant in the studied locations. These results, to some extent, are similar to those from riparian areas affected by hydropeaking in boreal streams (Bejarano et al., 2018) but differ from those from the Mediterranean and semi-arid regions, where drought-adapted species were clearly favoured (Catford, Morris, Vesk, Gippel, & Downes, 2014). This confirms that there are different scenarios of flow alteration that determine whether plant guilds and traits are favoured or disfavoured in riparian communities. These scenarios ultimately depend on the particular characteristics of the region, which define the water and energy needs and hence the specific operation modes of reservoirs. For instance, hydropeaking creates repetitive inundations along lower riparian areas to produce energy, and flow regulation is typically used in more arid regions to address a desynchronisation between water demand and the natural water cycle, resulting in water stress and lack of flood disturbance along riparian areas and floodplains. At the community level, the former triggers strong filtering towards easily dispersed, flexible, flood-tolerant, and amphibious plants (Bejarano et al., 2020), whereas the latter results in the encroachment of riparian vegetation and the territorialisation of the community (Bejarano & Sordo-Ward, 2011). Although both scenarios, hydropeaking and reservoir filling, appear to favour flood-tolerant species, they differ in that riparian plants along the Yangtze River suffer from overhead submergence spanning several months instead of short, frequent inundations.

According to Bejarano et al. (2020), the duration of the submergence period is key for seedling emergence, but once this stage has been overcome, the depth of inundation, through its effect on performance and survival, would ultimately filter out the species in the communities along the shores of the TGR. Further research on which particular flow features affect which particular life stages of plant species should be carried out in the future.

The selection of functional indexes considerably affects the interpretation of the functional responses of ecosystems following disturbance. However, no consensus has been reached regarding the most appropriate index (Lozanovska et al., 2018). In the present study, the reduction in the number of guilds and FRic suggested that some functional traits were lost. However, to what extent ecosystem functions would be lost is largely dependent upon the functional uniqueness and abundance of the lost species (Kuebbing et al., 2018). The maintenance of the abundant and functional guilds demonstrates the disparity between FDis and FRic because the former took trait abundance into account (Laliberté & Legendre, 2010). From this perspective, FDis provides a more reasonable interpretation than FRic and guild richness in our case.

5 | CONCLUSIONS

To our knowledge, this study is the first to investigate the functional response of riparian vegetation to unnaturally long flooding conditions upstream from a multifunctional giant dam. Riparian vegetation exhibited a high functional resilience to prolonged flooding induced by the TGR in view of maintaining the most abundant and functional guilds. This high resilience might have benefited from a long growing season under subtropical climate conditions, which facilitated a rapid recovery from disturbance. Including different life forms provides a more comprehensive understanding of the responses of riparian vegetation to flow alteration. Herbs, as predicted in previous studies, are sensitive to flow regulation even after the first year of dam filling. The useful outcomes that might be derived from our study for managers and decision makers are as follow. First, herb-dominated riparian vegetation is unlikely to be destroyed by intensified flooding under subtropical climate conditions, and this is important for predicting the changes in freshwater ecosystems in regions that might be subject to increased flooding risk and giant dam construction. Second, transregional trait databases for riparian plants including different life forms should be developed to make the effects of flow regulation on riparian vegetation comparable. Finally, flood-tolerant riparian herbs, which showed incredible flooding tolerance, are valuable resources for the restoration managers of riparian areas.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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SUPPORTING INFORMATION

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