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Subtropical reservoir shorelines have reduced plant species and functional richness compared with adjacent riparian wetlands

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Abstract

Dam construction has large negative effects on biodiversity in river and riparian ecosystems worldwide. This study aimed to determine whether reservoir shorelines had lower plant species diversity and functional diversity than unregulated or lightly regulated riparian wetlands and to examine the responses of plant diversity and functional traits to reservoir shoreline environmental gradients. We surveyed 146, 44, and 67 plots on reservoir shorelines and in mainstem and tributary riparian wetlands, respectively, in a subtropical river-reservoir system. Species richness, functional richness, evenness, and divergence were calculated to reflect the species and functional diversity of plant communities. Environmental factors including elevation above water level, slope, landform type, substrate, disturbance, and cover were measured. The results showed that both species and functional richness were significantly lower on reservoir shorelines than in riparian wetlands. The relative species number of clonal plants and relative cover of annual plants were both negatively related to slope and elevation. Structural equation modeling and other statistical analyses indicated that most environmental factors had significant effects on species and functional richness on reservoir shorelines but had no significant effect on functional evenness and divergence. Our findings suggest that reservoir shoreline wetlands formed by damming rivers and inundating pre-existing riparian wetlands can be a biodiversity coldspot in regulated rivers at the plot level. Topographic factors are important in determining the plant diversity and vegetation establishment on reservoir shorelines in the Yangtze River basin.

Keywords: Danjiangkou Reservoir, functional diversity, river regulation, structural equation modeling, Yangtze River

S Online supplementary data available from stacks.iop.org/ERL/8/044007/mmedia

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1. Introduction

Habitat conditions are generally recognized as the most important factors determining species diversity in riparian wetlands (Tiegs *et al* 2005). However, natural riparian habitats

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are strongly altered by river regulation and dam construction. By the end of the 20th century, about 45 000 large dams (>15 m in height) and over 800 000 small dams had been built on rivers worldwide (WCD 2000), resulting in habitat fragmentation and significant changes in the hydrological regime, sediment transport, and species migration in regulated rivers (Cogels *et al* 1997, Mallik and Richardson 2009, Catford *et al* 2011). These changes may have direct or indirect effects on plant diversity in riparian wetlands (Jansson *et al* 2000).

Although many studies have investigated the vegetation of riparian wetlands (e.g., Baattrup-Pedersen and Riis 1999, Murphy et al 2003), relatively few have focused on the species diversity of reservoir shorelines (Nilsson et al 1997, Luken and Bezold 2000, Topuzović et al 2009). Reservoirs formed by damming rivers and inundating riparian wetlands generally develop new shoreline wetlands between high and low water levels (Nilsson and Berggren 2000). Unlike riparian wetlands, reservoir shorelines experience large fluctuations between the low water levels in the rainy season for flood control and the high levels in the dry season for hydropower generation. For this reason, reservoir shorelines may be subjected to the most severe effects of dam construction among the wetlands in regulated rivers. Nilsson et al (1997) have indicated that species richness on reservoir shorelines is lower than that in similar sites along adjacent free-flowing rivers. Johnson (2002) has also proposed a hypothesis that reservoir shorelines have less species diversity than unregulated and lightly regulated wetlands (e.g., tributaries). Nevertheless, it is still unclear whether reservoir shorelines are a coldspot of biodiversity in regulated rivers.

There is increasing evidence that functional diversity is more important to vegetation stability and ecosystem function than species diversity (Tilman *et al* 1997, Walker *et al* 1999). In contrast to species diversity, functional diversity measures the value and range of functional traits of species present in a community, and it considers the complementarity and redundancy of co-occurring species (Díaz and Cabido 2001). Mason *et al* (2005) suggest that functional diversity can be described by functional richness, evenness and divergence, which determine different facets of functional diversity. These indices are calculated based on continuous (e.g., seed mass) or categorical functional traits (e.g., life form), and have been widely accepted and used in recent years (Pakeman 2011, Arthaud *et al* 2012).

Plant diversity in riparian wetlands is generally responsive to multiple environmental factors, such as substrate quality and flood disturbance (Pollock *et al* 1998, Murphy *et al* 2003). Given the importance of reservoir shorelines in protecting regional biodiversity and providing various ecosystem services (Liu *et al* 2011), it is surprising that few studies have been conducted to quantify the relationships between plant diversity and environmental factors on reservoir shorelines (Luken and Bezold 2000, Howard and Wells 2009). The association of increases in the slope of reservoir shorelines with decreases in species richness in an American reservoir suggests that topography, as well as other environmental factors that strongly influence species diversity in riparian wetlands, may play an important role in determining the plant diversity of reservoir shorelines (Luken and Bezold 2000).

The Yangtze River basin in China is one of the most highly developed river regulation areas, with more than 40 giant dams (e.g., the Three Gorges dam) and thousands of large dams built for flood control and hydropower generation. This study was conducted in a subtropical river-reservoir system in the Han River in the Yangtze River basin and focused on the plant diversity of the reservoir shorelines and riparian wetlands. The objectives of the study were (1) to compare the species and functional diversity of reservoir shorelines with those of adjacent riparian wetlands and to test the hypothesis proposed by Johnson (2002), (2) to examine the responses of plant functional traits to environmental gradients on reservoir shorelines, and (3) to quantify the direct and indirect effects of topography and other environmental factors on species and functional diversity on reservoir shorelines.

2. Methods

2.1. Study area

The Han River, originating in Ningqiang county in Shaanxi province, is the largest tributary of the Yangtze River, with a drainage area of approximately 159000 km² and a total length of 1577 km. Danjiangkou Reservoir (32°36'-33°48'N, 110°59'-111°49'E), one of the largest impoundments (water surface area 745 km² and reservoir storage 17.5 km³) in China, is located on the upper reach of the Han River and was formed in 1967 (figure 1). The area of reservoir shorelines between high and low water levels is approximately 300 km². The vegetation of the reservoir shorelines consists of terrestrial and amphibious species such as Cynodon dactylon, Abutilon theophrasti, Xanthium sibiricum, and Calystegia hederacea (Liu et al 2009). The climate of this region is subtropical monsoon, with a mean air temperature of 2.4 °C in January and 28.4 °C in July. The mean annual precipitation is approximately 804 mm, and 80% of the total rainfall is concentrated in the rainy season from May to October (Liu et al 2010). The highest water level in the Danjiangkou Reservoir generally occurs in winter for hydropower generation. The lowest water level always occurs in summer for flooding control. This pattern is the reverse of the natural hydrological regime of unregulated reaches in the Han River (figure S1, available at stacks.iop.org/ERL/8/ 044007/mmedia).

Vegetation (forest and shrub) is the dominant land use within the 1000-m riparian area in the upper Han River basin (Li *et al* 2012). Because the majority of the upper Han River reaches are incised, the riparian vegetation is restricted to a relatively narrow band. There are approximately 16 permanent or ephemeral tributaries around the Danjiangkou Reservoir. Most of the tributaries, characterized by sand and gravel substrates, are low-energy fluvial systems with a width of 2–10 m. The discharge of these tributaries is usually low, but the seasonal variation is similar to that of the Han River.



Figure 1. Locations of sampling transects in the subtropical river–reservoir system. (•) Reservoir shorelines; (\blacktriangle) mainstem riparian wetlands; (\blacksquare) tributary riparian wetlands.

Spring and summer floods are generally short but intense, and discharge is sensitive to rainfall. There are no hydrological stations or storage reservoirs on these tributaries, and the range of water level fluctuation is approximately 1-2 m.

2.2. Field surveys

A total of 17, 8, and 6 sampling transects were established on the reservoir shorelines, mainstem riparian wetlands, and tributary riparian wetlands, respectively, in summer (August 2006), when plant vegetative growth was near maximum (figure 1). In August 2008, we established ten additional sampling transects on the reservoir shorelines. Reservoir shoreline transects were reached primarily from a fishing boat; riparian wetland transects were reached by car, motorbike, or on foot. Because many riparian wetlands were difficult to reach by vehicle, the transect number was relatively low. All transects ran perpendicular to the flow and extended from the water's edge to the upper edge of the wetlands. Each transect was generally separated by a minimum distance of 3 km from neighboring transects. To avoid the effect of reservoir backwater, all upstream and tributary transects were established away from the backwater area. One or two transects on five permanent tributaries were selected based on riparian conditions and accessibility. Reservoir shoreline transects were located in the zone of water level fluctuations and were generally inundated in late autumn and winter; other transects were located in riparian marshes. The length of the sampling transects depended primarily on the wetland width and ranged from 2 m to more than 50 m.

Because there were few trees or shrubs in wetlands in the studied areas (Liu *et al* 2009), three or more plots $(1 \text{ m} \times 1 \text{ m})$ were surveyed along each transect at 1–3 m intervals based on the transect length and wetland types. A total of 257 plots were surveyed, of which 146 plots were surveyed on

reservoir shorelines, 44 plots in mainstem riparian wetlands, and 67 plots in tributary riparian wetlands. Plant cover was estimated by dividing each plot into 100 cells ($0.1 \text{ m} \times 0.1 \text{ m}$) with a 1 m \times 1 m grid frame and counting the number of cells occupied by each species. Cumulative plant cover was calculated by summing the cover of all species (Noe and Zedler 2001). The Flora of China (www.flora.ac.cn/) was used as the authority for identifying the plant species.

Three topographic factors (i.e., slope, relative elevation, and landform type), substrate and human disturbance were measured in the field to examine the effects of topography and other environmental factors on the species and functional diversity of reservoir shorelines. The slope perpendicular to the contour lines was measured in each plot from the reservoir shorelines with a clinometer. The elevation above water level was expressed as the height of each plot above the water surface of the reservoir and measured with a level and rod. The landform type around the sampling transects was classified into mountains and plains. The substrate was classified into five categories based on soil grain size and texture: clay, loam, sand (0.25-3 mm), gravel (3-30 mm), and boulder (diameter > 30 mm). Proximity to villages and roads, grazing lands, and sand extraction were included to assess human disturbance on a scale of 1 (mildly disturbed) to 3 (severely disturbed). These selected environmental factors have been found to affect the plant diversity in riparian wetlands and effectively reflect the environmental gradients of reservoir shorelines (Luken and Bezold 2000).

2.3. Calculation of plant diversity indices

We described the plant species diversity of the reservoir shorelines, mainstem riparian wetlands, and tributary riparian wetlands in terms of species richness (Chen *et al* 2012a). Richness was defined as the number of plant species per plot. Importance values were calculated for each plant species in a plot by averaging the species' relative cover and relative frequency. We used functional richness, evenness, and divergence to represent functional diversity (Mason *et al* 2005). Functional richness represents the amount of functional space occupied by the species of a community, functional evenness describes how evenly spread the species (or abundance) of a community are in functional space, and functional divergence measures the divergence in the distribution of species abundance in functional space (Pakeman 2011). The three indices measure different aspects of functional diversity and are usually approximated through measurements of species functional traits. To calculate the functional diversity indices, we used the FD package in R software version 2.15.0 (Laliberté and Shipley 2011).

Four categorical (i.e., growth form, life form, longevity, and clonality) and two continuous functional traits (seed mass and maximum plant height) closely associated with plant tolerance and adaptation to disturbance in riparian zones were selected to calculate the functional diversity indices (Stromberg 2007). Species were first classified into four growth form groups, i.e., graminoids, herbs, ferns, and shrubs or trees (seedlings/saplings). Within each life form, species were then grouped into three functional types (terrestrial, amphibious, and submerged species). For longevity and clonality, we used a binary classification of annual or perennial (including biennial) and clonal or non-clonal to divide species into different groups. The seed mass of most species was measured by weighing at least 100 air-dried seeds and calculating the mean weight for a single seed in October 2011. For other species that were not seeding, seed mass was primarily obtained from the Seed Information Database and the Chinese literature (Liu et al 2008, Chen et al 2012b). Maximum plant height was extracted from a local flora (Fu 2002).

2.4. Statistical analyses

We calculated two nonparametric estimators (ICE and Chao2) of total species number in the reservoir shorelines, mainstem riparian wetlands and tributary riparian wetlands after randomizing the sample order 100 times using the EstimateS software program (http://purl.oclc.org/estimates). Both estimators have been successfully used to reduce the bias in underestimating total species number when sample sizes are small (Muirhead *et al* 2006). To determine whether the cumulative species number differed significantly among the three wetland types, we also plotted plot-based rarefaction curves (Mao Tau function) with 95% confidence intervals using the EstimateS software program.

Prior to the statistical analyses, the data were checked for normality and ln or ln(x + 1)-transformed when necessary. A nested ANOVA (with transect nested within wetland type) was used to determine differences in plant diversity among the three wetland types. We then used a *T*-test and ANOVA with Tukey multiple comparisons to explore the influences of substrate, human disturbance, and landform type on plant diversity. Regression analyses



Tributary riparian wetlands

Figure 2. Shared and unique species in reservoir shorelines and riparian wetlands.

were performed to analyze the relationships between plant diversity and continuous environmental variables (slope, elevation, and cover). Structural equation modeling (SEM) was used to further examine the direct and indirect effects of all environmental variables on plant diversity (Grace and Pugesek 1997). The path coefficients, *R*-squared, direct and indirect effects, and model fit parameters were calculated in Mplus software version 6.1 (Muthén and Muthén, Los Angeles, California, USA) using a robust maximum likelihood estimator. The overall fit of the SEM model was assessed using the root mean square error of approximation (RMSEA), comparative fit index (CFI), Tucker Lewis index (TLI), and standardized root mean square residual (SRMR). Because functional richness, evenness, and divergence could not be calculated for communities with <3 functionally singular species, plots with fewer than three species were omitted from the T-test, ANOVA, regression, and SEM analyses.

3. Results

3.1. Species composition of reservoir shorelines and riparian wetlands

A total of 110 plant species were recorded in plots, of which 46 species were recorded in reservoir shorelines, 30 in mainstem riparian wetlands, and 87 in tributary riparian wetlands (table S1, available at stacks.iop.org/ERL/ 8/044007/mmedia). The total species numbers in reservoir shorelines and mainstem riparian wetlands predicted by the ICE estimator (52.39 and 31.05) were relatively higher than those predicted by the Chao2 estimator (51.09 and 30.41). The cumulative species curves leveled off rapidly after the thirtieth plot at both reservoir shorelines and mainstem riparian wetlands (figure S2, available at stacks.iop.org/ERL/ 8/044007/mmedia). For the tributary riparian wetlands, there was no indication that the species accumulation curve had reached an asymptote (figure S2).

A Venn diagram showed that 11 unique species were found in the reservoir shorelines and only 14 species were present in all three wetland types (figure 2). The percentage of terrestrial species in the reservoir shorelines was higher

Table 1. Percentages of species and abundance according to plant trait states for reservoir shorelines and riparian wetlands.

	Reservo	ir shorelines	Mainst W	em riparian etlands	Tributary riparian wetlands		
Trait	Species	Abundance	Species	Abundance	Species	Abundance	
Growth form							
Graminoids	45.65	85.95	43.33	54.60	28.74	63.55	
Herbs	52.17	13.25	53.33	45.10	59.77	33.82	
Ferns	0.00	0.00	0.00	0.00	3.45	0.36	
Shrubs or trees	2.17	0.80	3.33	0.30	8.05	2.27	
Life form							
Terrestrial	65.22	80.29	53.33	39.51	72.41	46.51	
Amphibious	34.78	19.71	40.00	60.07	26.44	53.40	
Submerged	0.00	0.00	6.67	0.42	1.15	0.09	
Longevity							
Annual	69.57	26.23	56.67	19.75	50.57	50.16	
Perennial	30.43	73.77	43.33	80.25	49.43	49.84	
Clonality							
Clonal	43.48	82.98	50.00	80.52	42.53	56.61	
Non-clonal	56.52	17.02	50.00	19.48	57.47	43.39	

than that in mainstem riparian wetlands but lower than that in tributary riparian wetlands (table 1). There were no submerged plants on the reservoir shorelines. Compared to riparian wetlands, reservoir shorelines had a higher percentage of annual species. Clonal plants were found in all wetland types but were much more prevalent in reservoir shorelines and mainstem riparian wetlands (table 1).

3.2. Plant diversity of reservoir shorelines and riparian wetlands

Both species and functional richness in reservoir shorelines were significantly lower than those in mainstem and tributary riparian wetlands (figure 3, table S2, available at stacks.iop.org/ERL/8/044007/mmedia). Functional evenness in reservoir shorelines was also lower than that in tributary riparian wetlands, but did not differ from that in mainstem riparian wetlands. There was no significant difference in functional divergence among the three wetland types (table S2 and figure 3). Species richness in reservoir shorelines and riparian wetlands was positively and significantly related to functional richness and evenness but not significantly correlated with functional divergence (figure 4).

3.3. Response of plant functional traits to environment on reservoir shorelines

The relative species number of amphibious plants (i.e., the number of amphibious species divided by the species richness in a plot) and the relative cover of amphibious plants (i.e., the cover of amphibious species divided by the total plant cover in a plot) on reservoir shorelines were both negatively related to elevation and slope (table 2). Interestingly, a higher relative number of clonal species (e.g., *Cynodon dactylon* and *Paspalum paspaloides*) was found in the plots with lower elevation and slope (table 2). Furthermore, the relative number and cover of graminoid and shrub or tree species tended to



Figure 3. Species and functional diversity (mean \pm SD) in reservoir shorelines and riparian wetlands. Different letters denote significant differences (P < 0.05).

be positively correlated with elevation, whereas the relative number and cover of herb species were negatively related to elevation (table 2).

3.4. Plant diversity related to environment of reservoir shorelines

Neither the species diversity indices nor the functional diversity indices for reservoir shorelines were significantly correlated with elevation (figure 5). The maximum species richness and functional richness were generally found in flat plots. Plant cover was slightly positively related to species and functional richness but negatively correlated with functional evenness (figure 5). Species and functional richness varied significantly among substrate and disturbance types (figure S3, available at stacks.iop.org/ERL/8/044007/mmedia). The highest richness was generally observed in plots with clay substrate and moderate disturbance, whereas the lowest richness was observed in plots with boulder substrate.

The RMSEA of 0.088, the CFI of 0.959, the TLI of 0.894, and the SRMR of 0.069 that we calculated indicated that the



Figure 4. Relationships between species and functional diversity in reservoir shorelines and riparian wetlands. Plots with less than three species were not included in these analyses.



Figure 5. Relationships between species and functional diversity and elevation above water level, slope, and cover for reservoir shorelines. Plots with less than three species were not included in these analyses.

Table 2. Correlations between relative species number of each plant trait state and environmental factors (A) and between relative cover of each plant trait state and environmental factors (B) on reservoir shorelines.

	Traits	Elevation	Slope	Cover		Traits	Elevation	Slope	Cover
(A)	Growth form				(B)	Growth form			
. ,	Graminoids	0.229 ^a	-0.080	0.116		Graminoids	0.211 ^a	-0.014	0.219 ^a
	Herbs	-0.255 ^b	0.078	-0.101		Herbs	-0.254 ^b	0	-0.210^{a}
	Shrubs or trees	0.208 ^a	0.014	-0.108		Shrubs or trees	0.208 ^a	0.014	-0.108
	Life form					Life form			
	Amphibious species	-0.243 ^b	-0.423 ^b	0.172		Amphibious species	-0.262 ^b	-0.449 ^b	0.174
	Terrestrial species	0.243 ^b	0.423 ^b	-0.172		Terrestrial species	0.262 ^b	0.449 ^b	-0.174
	Longevity					Longevity			
	Annual	-0.060	-0.253 ^b	0.020		Annual	-0.217^{a}	-0.198^{a}	-0.229^{a}
	Perennial	0.060	0.253 ^b	-0.020		Perennial	0.217 ^a	0.198 ^a	0.229 ^a
	Clonality					Clonality			
	Clonal	-0.264 ^b	-0.212^{a}	0.137		Clonal	-0.027	-0.097	0.353 ^b
	Non-clonal	0.256 ^b	0.201 ^a	-0.143		Non-clonal	0.027	0.097	-0.353 ^b

^a Significant at the 0.05 level.

^b Significant at the 0.01 level.

fit of the SEM model was adequate (figure 6). The SEM model showed that slope, disturbance and cover were significant explanatory variables for the species richness, functional richness, and functional evenness (figure 6). Landform type exerted a strong indirect effect on species richness, primarily via slope (table 3, figure 6).



Figure 6. Structural equation model depicting the direct and indirect effects of environmental factors on the species and functional diversity of reservoir shorelines. Numbers beside arrows are standardized path coefficients. Arrow widths are proportional to the standardized path coefficients. Estimates of the proportions of total variance explained are shown in bold for each diversity index. Nonsignificant paths were removed from the model.

Table 3. Summary of results from the structural equation model: standardized direct, indirect and total effects of environmental factors on the species and functional diversity of reservoir shorelines.

	Species richness			Func	Functional richness Func			tional evenness		Functional divergence		
	Direct effect	Indirect effect	Total effect	Direct effect	Indirect effect	Total effect	Direct effect	Indirect effect	Total effect	Direct effect	Indirect effect	Total effect
Elevation	-0.039 -0.351^{a}	_	-0.039 -0.351	0.090	-0.049 -0.065	0.041	0.026 -0.039	_	0.026 -0.039	0.155	_	0.155
Landform	-0.098	0.259 ^a	0.161	0.076		0.076	0.200	_	0.200	0.271	_	0.271
Substrate	-0.188	_	-0.188	-0.035		-0.035	0.047	0.206	0.253	-0.228	_	-0.228
Disturbance Cover	$0.083 \\ -0.084$	_	$0.083 \\ -0.084$	0.181 ^a 0.093	_	0.181 0.093	$-0.065 \\ -0.289^{a}$	_	$-0.065 \\ -0.289$	$-0.085 \\ -0.172$	_	$-0.085 \\ -0.172$

^a Significant at the 0.05 level; direct effect coefficients are equal to the path coefficients shown in figure 6, and total effects are the sum of direct and indirect effects.

4. Discussion

Globally, dam construction has had large negative effects on biodiversity in riparian ecosystems (Jansson et al 2000). In general, reservoirs permanently inundate pre-existing riparian vegetation and develop new shoreline vegetation in pre-existing uplands primarily through propagule input, often on poor soils and without a riparian seed bank (Johnson 2002). Hydrochory (propagule dispersal by water) through river networks is recognized as an important mechanism for the colonization and establishment of many riparian plant species (Boedeltje et al 2003, Liu et al 2009, Moggridge et al 2009). Because nearly 60% of the species present on reservoir shorelines can be found in tributary riparian wetlands (figure 2), our study implies that tributary riparian wetlands can act as a potential propagule source for species diversity restoration and plant community development on reservoir shorelines after dam closure.

Johnson (2002) proposed that reservoir shorelines had less plant diversity than other lightly regulated or unregulated habitats (e.g., unregulated headwaters, replenished tributaries and non-replenished tributaries) along regulated rivers. Consistent with this hypothesis, our study found that both the species richness and the functional richness of the plant communities of reservoir shorelines are lower than those of mainstem and tributary riparian wetlands (figure 3). To our knowledge, this study is the first to examine the functional diversity of plant communities on reservoir shorelines. The relatively low species and functional richness of reservoir shorelines may have several causes. First, the original vegetation in pre-riparian or pre-upland areas along the Danjiangkou Reservoir has been inundated and destroyed by increased water levels after the dam closure. Secondly, the regulated hydrology and substantial water level fluctuations (up to 10 m) of the reservoir may inhibit the seedling development of certain hydrophytes on the reservoir margins. In contrast to the hydrological regime of the river reaches, the water level of the Danjiangkou Reservoir is lowered in spring and summer for flood control (figure S1, available at stacks. iop.org/ERL/8/044007/mmedia), producing a relatively dry habitat on reservoir shorelines compared with riparian wetlands during the growing season of the plants. In part, this characteristic of the reservoir also explains the higher percentage of terrestrial species and the lack of submerged species on reservoir shorelines (table 1).

The mechanism governing the pattern of plant diversity on reservoir shorelines and other wetlands is complex and includes, at least, abiotic stress and species interactions (Murphy et al 2003, Stendera et al 2012). In this study, topographic factors, including slope and landform type, were identified as important determinants of the species richness and functional richness of reservoir shorelines (table 3, figure 5). Previous studies have documented that slope is an effective predictor factor of plant diversity in riparian forests (Lyon and Sagers 1998, Kumar et al 2006). Similarly, Luken and Bezold (2000) have shown that slope has a significant effect on vegetation composition and suitability for wetland plant species on the shorelines of the Cave Run Reservoir, USA. The steep exposed shorelines around the Danjiangkou Reservoir are susceptible to soil loss, and the resulting boulder or gravel substrates support a depauperate flora and low vegetation cover (figure S3, available at stacks.iop.org/ERL/ 8/044007/mmedia). The landform type can reflect the upland land use around the reservoir shorelines. The mountains and plains in the studied areas are primarily dominated by forests and farmlands, respectively. Furthermore, upland land use also implies the potential effect of the input of seeds and vegetative propagules from different terrestrial ecosystems on the vegetation of the reservoir shoreline (Houlahan et al 2006). Many weeds in the surrounding paddy fields and drainage ditches are wetland species, and their propagules can be easily dispersed to the reservoir shorelines by wind and water.

As a commonly used topographic factor, elevation above water level is frequently recognized as an indicator of both water availability and flooding stress in riparian ecosystems (Turner et al 2004, Tiegs et al 2005). The intermediate disturbance hypothesis predicts that plant diversity should be highest at intermediate levels of environmental stress or disturbance (Pollock et al 1998, Svensson et al 2007). However, the results of other studies are not consistent with this hypothesis and show that species richness decreases or increases along gradients of increasing disturbance (e.g., Deiller et al 2001). In our study, both species and functional richness were relatively but not significantly higher in the low-elevation plots (figure 5). One possible explanation for this result is that these plots were surveyed in August, when a lower water level is maintained in the Danjiangkou Reservoir to control flooding. Thus, water availability is a key factor influencing the seedling growth of hydrophyte species. Low-elevation plots can furnish relatively moist habitats to support hydrophyte growth, whereas moderateand high-elevation plots may form relatively dry environments that inhibit hydrophyte growth (see table 2). The present study also revealed that the relative cover of annual plants was negatively related to elevation (table 2). Low-elevation shorelines are more frequently exposed to flooding events. Previous work has reported that herbaceous wetlands with fluctuating water levels may be mainly dominated by annuals (Collins and Wein 1995).

Substrate type is a compound factor that reflects grain size, moisture, and nutrient content. In general, moisture and nutrients in smaller-grained substrates, such as loam and clay, are higher than those in coarser-grained substrates, such as sand and gravel. The effect of the substrate on plant diversity has been studied in riparian zones (Bornette *et al* 2001). In this study, we observed a significant increase in species and functional richness with substrate gradients from boulder to clay (figure S3, available at stacks.iop.org/ERL/8/ 044007/mmedia), and the relationship of substrate type with species richness represents a series of complex mechanisms interacting to determine species richness, including soil moisture and soil nutrients. Soil nutrients and moisture were not considered in this study because boulder and gravel substrate are difficult to analyze and because these characteristics can be indirectly reflected by substrate type and topography (Qiu et al 2001). Fine substrates, such as clay and loam, in riparian habitats usually indicate a weak scouring effect and silting processes (Bornette et al 2001). The occurrence of all boulder and gravel substrate in steeply sloping areas on the reservoir shorelines suggests that substrate may be severely affected by hydrological processes.

Plant richness has been found to be positively related to many ecological functions (e.g., primary production and nitrogen retention) in wetlands (Engelhardt and Ritchie 2002, Zhu et al 2012). Our findings suggest that reservoir shoreline wetlands can be a biodiversity coldspot in regulated rivers. To increase biodiversity and mitigate the adverse ecological impacts of dam construction, artificial vegetation restoration on reservoir shorelines has been performed at several large Chinese reservoirs (e.g., the Three Gorges Reservoir). Spontaneously colonizing species, which are naturally established in fluctuating water level areas, are adapted to survive in such an environment (Fraissé et al 1997). Therefore, the dominant herbaceous species of current reservoir shorelines can represent good candidates for revegetation in the Danjiangkou Reservoir and adjacent reservoirs. For the purpose of species protection, unique or rare species such as Sagittaria trifolia and Lindernia procumbens on the reservoir shorelines should also receive more attention during the revegetation process. Moreover, the results of this study not only indicate that slope and substrate can significantly affect species and functional richness of reservoir shorelines but also imply that we can increase the local plant diversity by reducing the slope of reservoir shorelines and improving substrate quality through the addition of clay and loam soils.

5. Conclusions

In this letter, we focus primarily on the species diversity and functional diversity of the plant communities of the reservoir shorelines and adjacent riparian wetlands in the Yangtze River basin, one of the most active areas of dam construction in the world. To our knowledge, this is the first time that the patterns and determinants of plant functional diversity in river–reservoir systems have been examined. Our study focuses on a single reservoir in the Yangtze River basin. However, dam construction is a global phenomenon. We argue that more studies are needed to explore the plant functional diversity in other highly developed river regulation areas (e.g., the Mississippi River basin).

The shoreline wetlands along the studied reservoir have lower species and functional richness than the adjacent riparian wetlands and can be a coldspot of biodiversity in regulated rivers at the plot scale. This finding is consistent with the proposed hypothesis. Slope and landform can directly or indirectly affect the species diversity but not functional diversity on reservoir shorelines. Based on the results of this study, we propose that dam construction would result in the decline of both species and functional richness (but not functional evenness and divergence) on reservoir shorelines and that slope was the key factor determining the plant diversity of reservoir shorelines in the Yangtze River basin of China.

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