Diversity and Distribution of Riparian Arthropods in the Drawdown Zone of China's Three Gorges Reservoir

Kehong Wang,^{1,2,e} Xingzhong Yuan,^{1,2,3} Guanxiong Zhang,^{1,2} Shuangshuang Liu,^{1,2} Fang Wang,^{1,2} Hong Liu,² Mengjie Zhang,^{1,2} and Lilei Zhou¹

¹Faculty of Architecture and Urban Planning, Chongqing University, Chongqing 400030, China, ²Key Laboratory of New Technology for Construction of Cities in Mountain Area, Ministry of Education, Chongqing University, Chongqing 400044, China, and ³Corresponding author, e-mail: 1072000659@qq.com

Subject Editor: Darrell Ross

Received 28 April 2019; Editorial decision 5 August 2019

Abstract

Riparian zones are interesting habitats as they are important transitional zones between terrestrial and aquatic ecosystems, but highly threatened by human disturbances. They support a high arthropod diversity as they experience periodic flooding disturbance and sharp environmental gradients. Their associated arthropod fauna are of high conservation value. Nevertheless, their arthropod diversity remains largely unknown, and its distribution pattern along elevational gradients is poorly understood. Few data are available on the effects of flood regimes and other factors in determining riparian arthropod communities. In this study, we investigated the diversity and distribution of riparian arthropods along an elevational gradient and determined the major factors structuring the arthropod communities in the drawdown zone of the Three Gorges Reservoir, China. Significant compositional and structural changes of riparian arthropods increased with elevation. The relative abundance of predators decreased with elevation, whereas the saprovores and omnivores showed an upward trend along the elevational gradient. Redundancy analysis showed that there were significant interactions between the flood regimes, plant communities, and soil conditions. Among these environmental factors studied, flood duration was the main factor in structuring the riparian arthropod communities. Conservation and restoration strategies should consider flood duration in the operation of large reservoirs because riparian arthropods are particularly sensitive to flood regimes.

Key words: drawdown zone, riparian arthropod, flooding, spatial distribution, the Three Gorges Reservoir

Arthropods are abundant and diverse in riparian zones of streams and play significant roles by influencing the structure and function of riparian ecosystems (Adis and Junk 2002). In particular, riparian arthropods provide an essential link of nutrient cycling and energy flow between aquatic and terrestrial ecosystems (Baxter et al. 2005, Paetzold et al. 2005, Larsen et al. 2016) and have been shown to be sensitive to changes in the hydrological regime and habitat conditions (Paetzold et al. 2008, Borer et al. 2012, Marx et al. 2012, Ramey and Richardson 2017). Therefore, riparian arthropods can be used as valuable indicators for the assessment, management, and restoration of river ecosystems.

Riparian zones, as critical ecological interfaces between terrestrial and aquatic ecosystems, are the most diverse, dynamic, and complex biophysical habitats (Naiman et al. 1993, Naiman and Décamps 1997, Décamps et al. 2009). Riparian habitats possess a highly dynamic and distinct arthropod community because they are characterized by periodic flooding and drought, enhanced water and nutrient availability, elevated microhabitat and vegetation diversity, sharp microclimate gradients, and unique food resources (Rykken et al. 2011, Ramey and Richardson 2017). Many studies have noted that riparian habitats increase regional species diversity by harboring unique species (Sabo et al. 2005b, Soykan et al. 2012). However, approximately 90% of all riparian zones worldwide have been artificially modified as they are heavily exploited for hydroelectric power generation, flood control, navigation, and irrigation (Tockner and Stanford 2002). Understanding the diversity and distribution patterns of riparian arthropods is important for the conservation and management of riparian zones.

Many studies have investigated the diversity and distribution patterns of riparian arthropod communities (Uetz et al. 1979, Davis et al. 2006, Meriste et al. 2016, Sánchez-Montoya et al. 2016, Ralston et al. 2017). These previous studies focused on a single habitat type, such as exposed sediments (Bates et al. 2007, McCluney and Sabo 2012), or on part of the vertical gradients (Steward et al. 2011, Soykan et al. 2012, Moody and Sabo 2017, Ralston et al. 2017). However, the entire vertical distribution pattern

All rights reserved. For permissions, please e-mail: journals.permissions@oup.com.

of riparian arthropod communities from the water's edge to maximum water level is poorly understood.

Riparian arthropod diversity and composition in riparian habitats are affected by flood regime (Molnár et al. 2009, Lessel et al. 2011, Sienkiewicz and Żmihorski 2012), riparian vegetation diversity and structure (Schaffers et al. 2008, Borer et al. 2012, Ebeling et al. 2018), soil moisture and nutrients (Sabo et al. 2005a, Entling et al. 2007, Henshall et al. 2011), and river topography (Fernández Campón 2014, Bednarska et al. 2018). In the drawdown zone of the Three Gorges Reservoir, the flood regimes are characterized by high water levels, long duration, and seasonal asynchrony, which are probably the strongest factors determining the composition, structure, and distribution pattern of riparian arthropod communities (Wang et al. 2014, Tong et al. 2018). However, there is little information about the riparian arthropod community responses to annual hydrological regime regulation in the drawdown zone of the Three Gorges Reservoir.

The drawdown zone of the Three Gorges Reservoir is a unique riparian landscape with a vertical height of 30 m and an area of approximately 348.9 km². The drawdown zone is characterized by high water levels, nutrient-rich soils, and a variable topographic gradient that includes wet meadows and relatively dry surfaces. The flood regimes of the drawdown zone are regulated by the Three Gorges Dam. The flood duration, depth, and frequency decrease with the elevation above sea level and are also related to the microtopography of the sampled site. Therefore, the drawdown zone of the Three Gorges Reservoir experiences sharp gradients of hydrological regimes and attracts many scholars and institutes to conduct experiments and long-term monitoring (Lü et al. 2015).

In this study, we investigated the composition, structure, and distribution pattern of riparian arthropod communities in the drawdown zone in the confluent area of the Pengxi River and the Baijia Stream. The drawdown zone also provides a unique model system for studying the arthropod community composition, diversity, and distribution patterns along the riparian vertical gradients. We examined the effect of environmental factors (e.g., flood regimes, plant characteristics, and soil properties) on the riparian arthropod communities. We hypothesized that flood regime, especially flood duration, may be the dominating force in structuring the community structure and distribution pattern of riparian arthropods in the drawdown zone of the Three Gorges Reservoir. Knowledge of the diversity and distribution patterns of arthropod fauna can help to improve conservation and restoration strategies in this drawdown zone.

Materials and Methods

Study Area

The study was carried out in the confluent area of the Pengxi River and the Baijia Stream (108°33′14.69″–108°33′33.43″ E, 31°08′14.95″–31°09′02.32″ N) located in the Pengxi River Wetland Nature Reserve of Chongqing Municipality, southwestern China. It covers 3.19 km² of continuous natural grasslands and characterized by sharp gradients of flood duration, depth, and frequency (Sun et al. 2010). The Pengxi River is a primary tributary upstream of the Yangtze River and is approximately 250 km upstream of the Three Gorges Dam (Fig. 1). The water level of the Baijia Stream reaches 175 m in November, recedes slowly to 145 m in May, and then rises rapidly after September. A brief summer flooding caused by heavy rainfalls in the upstream area of the Three Gorges Reservoir occurred in June or July. This area has an open and wide habitat and shows a sharp hydrological gradient. The vegetation was distributed zonally from the water edge to the highest water level and was dominated by bermudagrass (*Cynodon dactylon* L., Graminales: Gramineae), Siberian cocklebur (*Xanthium sibiricum* Patrin ex Widder, Asterales: Compositae), velvetleaf (*Abutilon theophrasti* Medicus, Malvales: Malvaceae), and bur beggarticks (*Bidens tripartita* L., Asterales: Compositae). The soil types were mainly sandy soil, purple soil, and paddy soil.

Arthropod Sampling

Riparian arthropods were sampled by pitfall traps four times at monthly intervals from late May to August 2017. The water level fluctuated primarily between 145 and 150 m in these sampling dates. At each sampling date, four transects located 200 m apart and perpendicular to the channel were established. For each transect, an elevation gradient consisting of six elevations (i.e., 150, 155, 160, 165, 170, and 175 m) was used to reflect the full range of the flood regime. At each elevation, five pitfall traps (500-ml plastic cup with a diameter of 9.5 cm and a height of 13.5 cm) were deployed linearly at 10-m intervals. Therefore, the sampling design included a total of 480 traps (four transects × six elevations per transect× fiver traps per elevation × four sampling dates). In total, 100 ml of saturated NaCl solution was added as a preservative, and several drops of diluted detergent were added to reduce the surface tension. Traps were left for five rain-free days. The arthropods from the five traps of each elevation of each transect were pooled and stored for further identification.

Arthropods were identified to family level and were classified into four feeding guilds (predacious, saprophagous, phytophagous, and omnivorous) using keys of Insect Taxonomy (Cai 2017), Pictorial Keys to Soil Animals of China (Yin 1998), and Taxonomy of Hexapoda (Yuan 2006). Saprovores mainly fed on plant litter (e.g., fallen leaves) and included detritivores, fungivores, coprophagous, and necrophagous. Phytovores were defined as taxa that fed on the sap, branches, leaves, and roots of plants. Predators included species that occasionally consumed organic matter and live prey. Omnivores in this article only consisted of Formicidae and Blattidae because of their various diets and high abundance. Collembola, Acarina, and aerial taxa were eliminated because pitfall traps are not the appropriate sampling method for these taxa (Corti and Datry 2014). Arthropod samples were oven-dried at 60°C to constant weight after identification to determine the arthropod biomass.

Environmental Factors

The flood regimes (i.e., flooding depth, duration, and frequency) of each gradient were calculated based on the daily water-level data of the Three Gorges Dam from September 2016 to August 2017 published by the China Three Gorges Corporation (http://www.ctg.com. cn/sxjt/sqqk/index.html). Plant characteristics of each elevation were determined using five $1 \times 1 \text{ m}^2$ quadrats after arthropod sampling. Each quadrat was deployed 0.2-0.5 m apart from pitfall trap to reduce the digging effects. The number of plant species and coverage (%) was recorded in the field (Fang et al. 2009). The aboveground biomass of the plants in each quadrat was measured by the harvesting method (Fang et al. 2009). For the analysis, five plant quadrats were averaged to determine the plant richness, coverage, and biomass of each elevation within each transect. Then, one soil sample was collected with a 38-cm soil corer in each quadrat. The five soil samples of each elevation were mixed and stored for further analysis. Soil moisture was determined by drying 10- to 20-g soil subsamples for 24 h at 105°C. The soil organic matter content was measured by the loss-on-ignition method using a muffle furnace for 12 h at

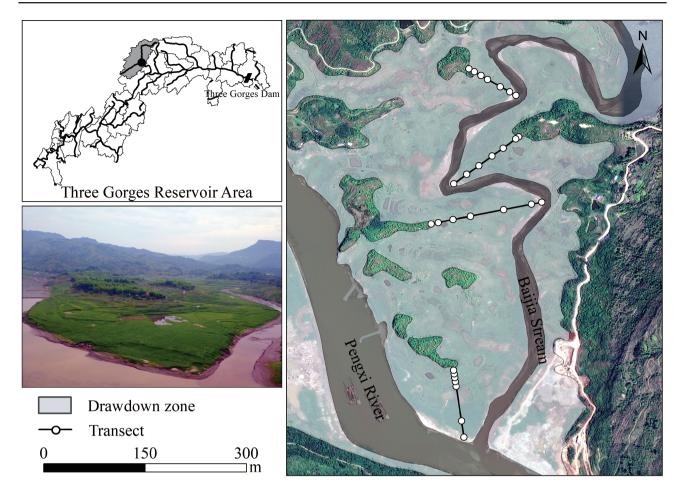


Fig. 1. Location of the study site and sketch map of sampling transects.

550°C. Soil temperature was measured by deploying geothermometers (5 cm underground) near a randomly selected trap of each gradient.

Data Analysis

A generalized linear model (GLM) was used to test the effects of elevation on the richness, abundance, Shannon diversity index, and biomass of the arthropod communities, as well as the relative abundance of four feeding guilds of riparian arthropods. Whenever significant *F*-values were obtained from GLM, we carried out post hoc analysis for multiple comparisons between means using Tukey's HSD tests. Both analyses were carried out with SPSS v. 20.0 (IBM, New York, NY). Before analyses, abundance values were averaged by four sampling dates for each elevation, as we were interested in the vertical distribution patterns of riparian arthropods, rather than seasonal variations. The final sample size was of six elevations across four transects (n = 24).

Permutational multivariate analysis of variance was used to determine the variation of arthropod community composition along elevation gradients. Cluster analysis was used to visualize the variation in arthropod community composition among different elevations. Both analyses were performed with PRIMER v. 5.0 based on the Bray–Curtis dissimilarity index of the abundance data after log(x + 1) transformed (Anderson et al. 2008).

The relationship between arthropod communities and environmental factors was explored using CANOCO v. 5.0 (Šmilauer and Lepš 2014). Detrended correspondence analysis was performed to determine the gradient lengths of the data set. Because the maximum length of gradient was 1.8, redundancy analysis (RDA) was carried out to test the strength of correlations between arthropod community composition and environmental factors. Monte Carlo permutation tests (999 permutations) were used to determine the significance of the obtained canonical axes. In addition, variation partitioning analysis with three groups (i.e., flooding, plant, and soil) was performed to test the importance of each group in influencing the composition of riparian arthropod communities. The relative contribution of each environmental factor or group to the explained variation of arthropod composition was determined by the inertia from the conditional effects based on Bonferroni correction. These analyses were based on the abundance data after log(x + 1) transformation. The rare taxa, for which relative abundance was less than 0.1%, were removed before analysis to minimize the influence of statistical artifacts (McCune et al. 2002).

Results

Environmental Factors

All nine environmental factors varied with elevation (Table 1). The flooding duration of the drawdown zone ranged from 61 to 295 d/yr. The flooding frequencies of the 150- and 155-m elevations were higher than those of the other elevations due to unpredictable summer flooding. Plant species richness increased at higher elevations, but plant coverage and biomass decreased.

Table 1. Environmental factors at each elevation in the drawdown zone of the Three Gorges Reservoir

Groups	Factors	150 m	155 m	160 m	165 m	170 m	175 m
Flooding	Duration (d/yr)	295	258	230	186	131	61
	Depth (m)	25	20	15	10	5	0
	Frequency (times/yr)	3	2	1	1	1	1
Plant	Biomass (g/m ²)	513.3 ± 77.7	1064.2 ± 103.8	1186.7 ± 263.4	1013.0 ± 80.4	842.3 ± 166.3	600.0 ± 35.6
	Coverage (%)	87.5 ± 3.2	89.6 ± 3.9	89.2 ± 2.8	79.2 ± 5.0	74.2 ± 7.2	58.8 ± 4.9
	Richness (species/m ²)	3.4 ± 0.4	2.3 ± 0.2	3.7 ± 0.5	6.3 ± 0.8	7.1 ± 1.2	10.8 ± 1.4
Soil	Moisture (%)	39.9 ± 1.1	31.8 ± 5.3	27.5 ± 6.6	15.6 ± 2.4	15.5 ± 4.1	12.2 ± 3.5
	Temperature (°C)	27.5 ± 0.7	25.7 ± 0.7	28.6 ± 0.9	26.2 ± 0.8	25.9 ± 0.9	28.2 ± 0.9
	Organic matter (g/kg)	57.0 ± 3.4	61.0 ± 3.7	70.5 ± 4.1	66.9 ± 4.4	62.7 ± 3.7	57.8 ± 2.4

	Elevation (m)	Flooding duration (d/yr)	Flooding depth (m)	Flooding frequency (times/yr)	Plant biomass (g/m ²)	Plant coverage (%)	Plant richness (species/m)	Soil moisture (%)	Soil temperature (°C)	Soil organic matter (g/kg)
Elevation (m)	1.00									
Flooding duration (d/yr)	-0.99**	1.00								
Flooding depth (m)	-1.00**	0.99**	1.00							
Flooding frequency (times/yr)	-0.83**	0.74**	0.83**	1.00						
Plant Biomass (g/m ²)	-0.06	0.15	0.06	-0.33	1.00					
Plant coverage (%)	-0.71**	0.76**	0.71**	0.41*	0.26	1.00				
Plant richness (species/m ²)	0.81**	-0.84**	-0.81**	-0.52**	-0.36	-0.82**	1.00			
Soil moisture (%)	-0.78**	0.75**	0.78**	0.71**	-0.04	0.38	-0.49*	1.00		
Soil Temperature (°C	C) 0.07	-0.10	-0.07	-0.06	-0.14	-0.13	0.18	0.07	1.00	
Soil organic matter (g/kg)	0.03	0.06	-0.03	-0.36	0.21	0.21	-0.14	-0.16	0.05	1.00

*P < 0.05, **P < 0.01.

Table 3. Mean abundance of the dominant taxa at each elevation in the drawdown zone the Three Gorges Reservoir

Dominant taxa	150 m	155 m	160 m	165 m	170 m	175 m
Carabidae	26.88 ± 6.19	12.56 ± 2.64	8.00 ± 2.60	4.13 ± 0.92	4.63 ± 0.46	4.19 ± 1.74
Staphylinidae	11.81 ± 1.54	5.13 ± 1.01	4.25 ± 1.95	4.13 ± 0.60	2.31 ± 0.57	1.88 ± 0.24
Pselaphidae	0.31 ± 0.12	2.00 ± 0.78	5.50 ± 2.49	14.13 ± 5.98	10.13 ± 3.96	2.00 ± 0.43
Araneidae	1.63 ± 0.26	3.25 ± 0.60	2.13 ± 0.77	5.69 ± 0.69	1.75 ± 0.41	0.69 ± 0.34
Lycosidae	24.31 ± 9.15	19.50 ± 7.94	13.06 ± 4.88	8.13 ± 4.69	6.69 ± 1.26	5.69 ± 1.07
Linyphiidae	7.69 ± 1.51	12.63 ± 2.39	14.81 ± 3.51	27.25 ± 3.36	11.06 ± 2.97	1.00 ± 0.44
Gryllidae	8.75 ± 2.24	13.56 ± 3.36	21.81 ± 8.40	18.81 ± 4.89	14.44 ± 3.96	10.00 ± 2.69
Tetrigidae	1.63 ± 1.29	1.00 ± 0.62	0.81 ± 0.56	0.75 ± 0.44	3.31 ± 1.74	2.69 ± 0.80
Formicidae	0.31 ± 0.16	3.94 ± 3.85	12.13 ± 8.36	15.19 ± 12.10	19.69 ± 3.86	104.31 ± 29.26
Porcellionidae	0.13 ± 0.07	0.25 ± 0.18	5.44 ± 3.63	12.19 ± 6.05	45.75 ± 13.71	41.75 ± 9.30
Paradoxosomatidae	7.50 ± 2.41	10.88 ± 8.15	9.88 ± 3.79	14.25 ± 6.88	40.06 ± 5.20	62.94 ± 5.17

Soil moisture increased with elevation. Soil temperature and organic matter showed the highest values at the 160-m elevation. Generally, the flooding duration, depth and frequency, plant coverage, and soil moisture were significantly negatively correlated with elevation (P < 0.01), but plant richness was significantly positively correlated with elevation (P < 0.01; Table 2). In addition, there were strong correlations between plant and soil characteristics and flood regimes. Plant coverage and soil moisture were significantly positively correlated with flood duration, frequencies, and depth (P < 0.05), but plant species richness was significantly negatively correlated (P < 0.01; Table 2). Plant species richness was significantly negatively correlated with soil moisture (P < 0.05; Table 2).

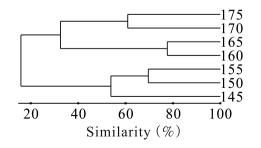


Fig. 2. Cluster analysis based on the Bray–Curtis percentage dissimilarity of the riparian arthropod communities at different elevations based on pooled data from four sampling dates.

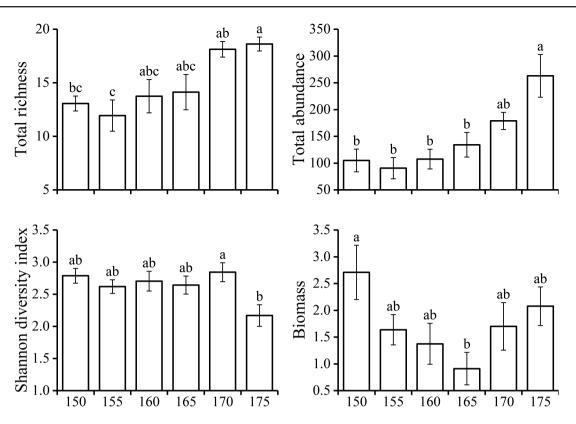


Fig. 3. Total richness, abundance, Shannon diversity index, and biomass of riparian arthropods across an elevation gradient in the drawdown zone of the Three Gorges Reservoir. Different letters indicate statistically significant differences based on Turkey's HSD tests.

Arthropod Community Composition

In total, 14,058 arthropods representing 82 families were trapped. The dominant taxa were spiders (Araneae, 20.42% of all individuals), beetles (Coleoptera, 19.26%), ants (Hymenoptera, 17.71%), millipedes (Polydesmida, 16.56%), pillworms (Isopoda, 12.01%), and crickets (Orthoptera, 9.94%). The richest taxa were beetles (35 families), followed by spiders (20 families). The number of each family was exhibited in Supp Appendix S1 (on-line only).

The community composition of riparian arthropods varied significantly with elevation (F = 18.08, $R^2 = 0.25$, P < 0.001). The arthropods exhibiting the highest abundance at 150, 155, 160, 165, 170, and 175 m were Carabidae, Lycosidae, Gryllidae, Linyphiidae, Porcellionidae, and Formicidae, respectively. The abundances of Porcellionidae, Formicidae, and Paradoxosomatidae were positively correlated with elevation, whereas the abundances of Carabidae, Staphylinidae, and Lycosidae were negatively correlated with elevation (Table 3). Cluster analysis (Fig. 2) showed a major break in similarity between elevations above 160 m and below 155 m (similarity only 20%).

Arthropod Richness, Abundance, Diversity, and Biomass

We observed significant effects of elevation on the richness, abundance, and diversity of riparian arthropods (P < 0.05), but not biomass (P > 0.05). Arthropod richness and abundance showed the same tendencies and were positively correlated with elevation above 150 m (Fig. 3). The arthropod richness ranged from 5 to 25 families and was highest (18.63 ± 0.65 families) at 175 m. The arthropod abundance ranged from 23 to 524 individuals and was also highest (262.88 ± 39.80 individuals) at 175 m. The highest Shannon diversity index (2.84 ± 0.15) was recorded at 170 m and the lowest

 (2.17 ± 0.17) at 175 m. The biomass was highest $(2.71 \pm 0.51$ g) at 150 m and showed a significant shift at 165 m.

Arthropod Feeding Guilds

The drawdown zone was dominated by saprovores and predators (Fig. 4). The relative abundance of saprovores, omnivores, and predators was significantly affected by elevation (P < 0.001), but not phytovores (P > 0.05). The relative abundance of predators decreased with elevation, whereas the saprovores and omnivores showed an upward trend with elevation (Fig. 4). The phytovores showed the highest relative abundance at 160 m, versus the lowest at 175 m (Fig. 4).

Relationship between Environmental Variables and Arthropod Community Composition

The RDA revealed the environmental gradients in the drawdown zone (Fig. 5). RDA showed that the first two axes explained 63.3% of the variation in the arthropod community composition (51.7% based on axis 1 and 11.6% based on axis 2). There was a strong correlation between arthropods and environmental factors, with correlations of 0.9739 (axis 1) and 0.9130 (axis 2).

All three environmental factor groups examined explained collectively 76.3% of the variation in the arthropod community composition. Of these variations explained by the RDA, 55.6% were caused by flooding, 43.9% by plants, and 29.4% by soil (Table 4). There were strong interactions between the three environmental factor groups. The explanation was 38.5% provided by the interaction between the plants and other two factor groups, and 37.5% by flooding and others. The results indicated that the interactions of the three factor groups were important pathways in determining the

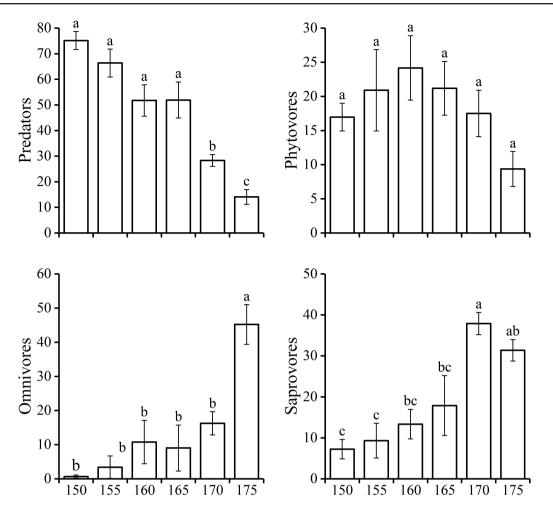


Fig. 4. Relative abundance of four feeding guilds of riparian arthropods across elevation gradients in the drawdown zone of the Three Gorges Reservoir. Different letters indicate statistically significant differences based on Turkey's HSD tests.

distribution of arthropod communities. Furthermore, the results also suggested that flooding regime was the main factor group that influenced the arthropod communities in the drawdown zone.

Of the total variation explained by the RDA, 59.7% was caused by flooding duration, 5.1% by flooding depth, 4.4% by flooding frequency, 11.1% by soil moisture, 9.0% by soil organic matter, 3.6% by soil temperature, 2.3% by plant biomass, 2.3% by plant richness, and 2.5% by plant coverage during the forward section process (Table 5). Only the conditional effects of flooding duration (F = 18.41, P < 0.01), soil moisture (F = 3.85, P < 0.01), soil organic matter (F = 3.48, P < 0.01), flooding depth (F = 2.10, P < 0.05), and flooding frequency (F = 1.97, P < 0.05) were significant in the Monte Carlo permutation test. The results of the RDA indicated that flooding duration was the best explanatory variable.

Discussion

Diversity and Composition of Riparian Arthropods in the Drawdown Zone

In total, we collected 82 families of riparian arthropods from the drawdown zone. The result indicated that the drawdown zone of the Three Gorges Reservoir supported a relatively high arthropod biodiversity compared with other studies in riparian zones (Xiao and Yue 2016, Ralston et al. 2017, Wang et al. 2019). The dominant taxa in the drawdown zone were ants, millipedes, spiders,

and beetles, which are also common in other highly disturbed riparian habitats (Uetz et al. 1979, Adis and Junk 2002, Sánchez-Montoya et al. 2016, Ralston et al. 2017). The most abundant arthropod feeding groups across the six elevations were predators and saprophagous arthropods. The drawdown zone of the Three Gorges Reservoir is subject to periodic flood disturbance and has relatively high plant productivity and wet soil conditions (Table 1). These conditions were known to support highly diverse arthropod communities (Pétillon et al. 2008, Ramey and Richardson 2017).

Distribution of Riparian Arthropods along the Elevational Gradient in the Drawdown Zone

We found that in the drawdown zone, there were significant compositional and structural changes of riparian arthropod communities along the elevational gradients. Our results indicated a clear pattern that arthropod richness and abundance increased with elevation. Similar patterns have also been reported in many previous studies (Uetz et al. 1979, Yuen and Dudgeon 2015, Meriste et al. 2016). This distribution pattern of arthropod communities might be closely related to flood regimes, plant communities, and soil conditions (Borer et al. 2012, Meriste et al. 2016).

Elevation in our study can be considered as a proxy of the flooding, plant, and soil characteristics. This is supported by our finding that flooding duration, depth, and frequency and soil moisture decreased

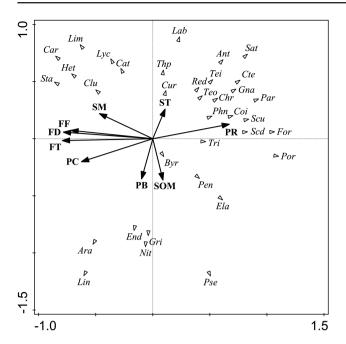


Fig. 5. Redundancy analysis (RDA) diagram showing the relationship between arthropod community composition and environmental factors in the drawdown zone of the Three Gorges Reservoir. The arthropod taxa shown are Anthicidae (Ant), Araneidae (Ara), Byrrhidae (Byr), Carabidae (Car), Catantopidae (Cat), Chrysomelidae (Chr), Clubionidae (Clu), Corinnidae (Coi), Ctenidae (Cte), Curculionidae (Cur), Elateridae (Ela), Endomychidae (End), Formicidae (For), Gnaphosidae (Gna), Gryllidae (Gri), Heteroceridae (Het), Labiduridae (Lab), Limnichidae (Lim), Linyphiidae(Lin), Lycosidae (Lyc), Nitidulidae (Nit), Paradoxosomatidae (Par), Pentatomidae (Pen), Phalangodidae (Phn), Porcellionidae (Por), Pselaphidae (Pse), Reduviidae (Red), Salticidae (Sat), Scutigeridae (Scu), Scydmaenidae (Scd), Staphylinidae (Sta), Tetrigidae (Tei), Tettigoniidae (Teo), Thripidae (Thp), and Tridactylidae (Tri). The environmental factors are flooding depth (FD), flooding duration (FT), flooding frequency (FF), plant biomass (PB), plant coverage (PC), plant richness (PR), soil moisture (SM), soil organic matter (SOM), and soil temperature (ST).

Table 4. Variation partitioning results for quantifying the con-ditional effects of the three environmental factor groups on thearthropod community composition in the drawdown zone of theThree Gorges Reservoir

Environmental factor groups	Explanation (%)	Explanation by pure factor group (%)	Explanation by crossing one and two other factor	
			groups	
Flooding	55.6	18.1	37.5	
Soil	29.4	14.2	15.2	
Plant	43.9	5.4	38.5	

significantly with elevation (Table 1). A number of studies have reported that flooding duration, depth, and frequency are negatively related to arthropod richness and abundance and have a selective effect on different taxa (Uetz et al. 1979, Desender and Maelfait 1999, Lambeets et al. 2009, Lafage et al. 2015). For example, the abundance of Carabid beetles and Lycosoid spiders decreased with elevation, but ants increased. Uetz et al. (1979) reported that the abundance of Carabid beetles and spiders decreased with elevation in Sangamon River in United States. Ballinger et al. (2007) found that the abundance of ants increased with elevation in Southern Australian floodplains.

Table 5. Redundancy analysis for quantifying the explanatory ability of the nine environmental factors with respect to the arthropod community composition in the drawdown zone of the Three Gorges Reservoir

Factor	Explanation %	Contribution %	Pseudo-F	Р
Flooding duration	45.6	59.7	18.41	0.002
Soil moisture	8.4	11.1	3.85	0.002
Soil organic matter	6.8	9.0	3.48	0.006
Flooding depth	3.9	5.1	2.10	0.012
Flooding frequency	3.4	4.4	1.97	0.040
Soil temperature	2.7	3.6	1.51	0.114
Plant biomass	1.8	2.3	1.05	0.390
Plant richness	1.7	2.3	1.01	0.426
Plant coverage	1.9	2.5	1.12	0.380

The Riparian Arthropod Community Depends on the Flood Regimes in the Drawdown Zone

Although the environmental factors influencing riparian arthropod communities were not comprehensive, the RDA indicated that flooding duration was the major factors that influenced the distribution and community structure of riparian arthropods among the different environmental factors studied in the drawdown zone (Tables 4 and 5). This result indicated that flood regimes might be the structural force in determining the arthropod communities in the drawdown zone.

Different elevations with varying flooding duration, depth, and frequency were generally reflected by variations in arthropod community composition and structure. Due to the differences in flooding tolerance, the different taxa of riparian arthropods responded differently along the elevational gradients. The lower area of the drawdown zone was dominated by predators, such as Carabid beetles and Lycosoid spiders, and the upper area consisted of saprophagous and omnivores, such as ants and millipedes. A number of studies have also shown that relatively flood-tolerant species are mainly found at lower elevations, where flooding is more prolonged, frequent, and unpredictable and that relatively flood-sensitive taxa are mainly distributed at the higher elevations, where the impacts of flooding are limited (Ballinger et al. 2005, Sánchez-Montoya et al. 2016, Ralston et al. 2017). Ballinger et al. (2005) demonstrated that the abundance, species richness, and biomass of beetles were greatest at sites that had been inundated for the longest period compared with nonflooded or briefly flooded sites. The results indicated that artificial flooding by the Three Gorges Dam might promote the diversity of predatory arthropods (e.g., ground beetles and spiders) by providing conditions that create a pulse in populations in the short term and reducing others, such as ants (Ballinger et al. 2007).

Conclusion

Riparian zones are interesting and threatened habitats, and their associated arthropod fauna are of high conservation value. The drawdown zone of the Three Gorges Reservoir supported a relative high arthropod biodiversity. The arthropod community composition and structure differed significantly with elevations. The riparian arthropod community and diversity change significantly under drastic human disturbances, such as dam construction. Therefore, more attention should be paid to investigating and monitoring the diversity and distribution pattern of riparian arthropod communities. The flooding duration of the Three Gorges Reservoir was the major factor shaping the arthropod communities among the nine environmental factors. Knowledge of riparian biodiversity and its impact factors can help to improve conservation and restoration strategies in the drawdown zone of large reservoirs.

Supplementary Material

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (grant number 51179214). We thank the Pengxi River Wetland Nature Reserve Management Bureau and the Pengxi River Wetland Research Station for their assistance in our research.

References Cited

- Adis, J., and W. J. Junk. 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. Freshw. Biol. 47: 711–731.
- Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E Ltd, Plymouth, United Kingdom.
- Ballinger, A., R. M. Nally, and P. S. Lake. 2005. Immediate and longer-term effects of managed flooding on floodplain invertebrate assemblages in south-eastern Australia: generation and maintenance of a mosaic landscape. Freshw. Biol. 50: 1190–1205.
- Ballinger, A., P. S. Lake, and R. M. Nally. 2007. Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. Oecologia 152: 227–238.
- Bates, A., J. Sadler, J. Perry, and A. Fowles. 2007. The microspatial distribution of beetles (Coleoptera) on exposed riverine sediments (ERS). Eur. J. Entomol. 104: 479–487.
- Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw. Biol. 50: 201–220.
- Bednarska, A. J., B. Wyżga, P. Mikuś, and R. Kędzior. 2018. Ground beetle communities in a mountain river subjected to restoration: the Raba River, Polish Carpathians. Sci. Total Environ. 610–611: 1180–1192.
- Borer, E. T., E. W. Seabloom, D. Tilman, and V. Novotny. 2012. Plant diversity controls arthropod biomass and temporal stability. Ecol. Lett. 15: 1457–1464.
- Cai, B. 2017. Insect taxonomy, rev. ed. Chemical Industry Press, Beijing, China. (in Chinese)
- Corti, R., and T. Datry. 2014. Drying of a temperate, intermittent river has little effect on adjacent riparian arthropod communities. Freshw. Biol. 59: 666–678.
- Davis, C. A., J. E. Austin, and D. A. Buhl. 2006. Factors influencing soil invertebrate communities in riparian grasslands of the central Platte River floodplain. Wetlands 26: 438–454.
- Décamps, H., R. J. Naiman, and M. E. McClain. 2009. Riparian zones, pp. 396–403. *In* G. E. Likens (ed.), Encyclopedia of inland waters. Academic Press, Oxford, MS.
- Desender, K., and J.-P. Maelfait. 1999. Diversity and conservation of terrestrial arthropods in tidal marshes along the River Schelde: a gradient analysis. Biol. Conserv. 87: 221–229.
- Ebeling, A., J. Hines, L. R. Hertzog, M. Lange, S. T. Meyer, N. K. Simons, and W. W. Weisser. 2018. Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. Basic Appl. Ecol. 26: 50–63.
- Entling, W., M. H. Schmidt, S. Bacher, R. Brandl, and W. Nentwig. 2007. Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. Global Ecol. Biogeogr. 16: 440–448.
- Fang, J., X. Wang, Z. Shen, Z. Tang, J. He, D. Yu, Y. Jiang, Z. Wang, C. Zheng, J. Zhu, and Z. Guo. 2009. Methods and protocols for plant community inventory. Biodiv. Sci. 17: 533–548. (in Chinese)

- Fernández Campón, F. 2014. Substrate preference in a colonial spider: is substrate choice affected by color morph? Entomol. Sci. 17: 130–133.
- Henshall, S. E., J. P. Sadler, D. M. Hannah, and A. J. Bates. 2011. The role of microhabitat and food availability in determining riparian invertebrate distributions on gravel bars: a habitat manipulation experiment. Ecohydrology 4: 512–519.
- Lafage, D., C. Sibelle, J. Secondi, A. Canard, and J. Pétillon. 2015. Shortterm resilience of arthropod assemblages after spring flood, with focus on spiders (Arachnida: Araneae) and carabids (Coleoptera: Carabidae). Ecohydrology 8: 1584–1599.
- Lambeets, K., M. L. Vandegehuchte, J.-P. Maelfait, and D. Bonte. 2009. Integrating environmental conditions and functional life-history traits for riparian arthropod conservation planning. Biol. Conserv. 142: 625–637.
- Larsen, S., J. D. Muehlbauer, and E. Marti. 2016. Resource subsidies between stream and terrestrial ecosystems under global change. Glob. Chang. Biol. 22: 2489–2504.
- Lessel, T., M. Marx, and G. Eisenbeis. 2011. Effects of ecological flooding on the temporal and spatial dynamics of carabid beetles (Coleoptera, Carabidae) and springtails (Collembola) in a polder habitat. ZooKeys 100: 421–446.
- Lü, M. Q., S. J. Wu, C. D. Chen, Y. Jiang, Z. F. Wen, J. L. Chen, Y. Wang, X. X. Wang, and P. Huang. 2015. A review of studies on water level fluctuating zone (WLFZ) of the Three Gorges Reservoir (TGR) based on bibliometric perspective. Acta Ecol. Sin. 35: 3504–3518. (in Chinese)
- Marx, M. T., P. Guhmann, and P. Decker. 2012. Adaptations and predispositions of different Middle European Arthropod Taxa (Collembola, Araneae, Chilopoda, Diplopoda) to flooding and drought conditions. Animals (Basel) 2: 564–590.
- McCluney, K. E., and J. L. Sabo. 2012. River drying lowers the diversity and alters the composition of an assemblage of desert riparian arthropods. Freshw. Biol. 57: 91–103.
- McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities, vol. 28. MjM Software Design, Gleneden Beach, OR.
- Meriste, M., A. Helm, and M. Ivask. 2016. Ground-dwelling spider fauna of flooded Meadows in Matsalu, Estonia. Wetlands 36: 525–537.
- Molnár, Á., Z. Csabai, and B. Tóthmérész. 2009. Influence of flooding and vegetation patterns on aquatic beetle diversity in a constructed wetland complex. Wetlands 29: 1214–1223.
- Moody, E. K., and J. L. Sabo. 2017. Dissimilarity in the riparian arthropod communities along surface water permanence gradients in aridland streams. Ecohydrology 10: e1819.
- Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. Annu. Rev. Ecol. Syst. 28: 621–658.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecol. Appl. 3: 209–212.
- Paetzold, A., C. J. Schubert, and K. Tockner. 2005. Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. Ecosystems 8: 748–759.
- Paetzold, A., C. Yoshimura, and K. Tockner. 2008. Riparian arthropod responses to flow regulation and river channelization. J. Appl. Ecol. 45: 894–903.
- Pétillon, J., A. Georges, A. Canard, J.-C. Lefeuvre, J. P. Bakker, and F. Ysnel. 2008. Influence of abiotic factors on spider and ground beetle communities in different salt-marsh systems. Basic Appl. Ecol. 9: 743–751.
- Ralston, B. E., N. S. Cobb, S. L. Brantley, J. Higgins, and C. B. Yackulic. 2017. Taxonomic and compositional differences of ground-dwelling arthropods in riparian habitats in Glen Canyon, Arizona, USA. West. N. Am. Nat. 77: 369–384.
- Ramey, T. L., and J. S. Richardson. 2017. Terrestrial invertebrates in the riparian zone: mechanisms underlying their unique diversity. BioScience 67: 808–819.
- Rykken, J. J., P. C. Jepson, and A. R. Moldenke. 2011. Ground-dwelling arthropod distribution and movement across a fragmented riparian forest. Northw. Sci. 85, 527–541.
- Sabo, J. L., C. U. Soykan, and A. Keller. 2005a. Functional roles of leaf litter detritus in terrestrial food webs, pp. 211–222. *In* P. de Ruiter, V. Wolters, J. C. Moore, and K. Melville-Smith (eds.), Dynamic food webs. Academic Press, Burlington, MA.

- Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and J. Welter. 2005b. Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86: 56–62.
- Sánchez-Montoya, M. D. M., D. von Schiller, A. Ruhí, G. S. Pechar, L. Proia, J. Miñano, M. R. Vidal-Abarca, M. L. Suárez, and K. Tockner. 2016. Responses of ground-dwelling arthropods to surface flow drying in channels and adjacent habitats along Mediterranean streams. Ecohydrology 9: 1376–1387.
- Schaffers, A. P., I. P. Raemakers, K. V. Sýkora, and C. J. Ter Braak. 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89: 782–794.
- Sienkiewicz, P., and M. Żmihorski. 2012. The effect of disturbance caused by rivers flooding on ground beetles (Coleoptera: Carabidae). Eur. J. Entomol. 109: 535–541.
- Šmilauer, P., and J. Lepš. 2014. Multivariate analysis of ecological data using Canoco 5, 2nd ed. Cambridge University Press, Cambridge, United Kingdom.
- Soykan, C. U., L. A. Brand, L. Ries, J. C. Stromberg, C. Hass, D. A. Simmons, Jr, W. J. Patterson, and J. L. Sabo. 2012. Multitaxonomic diversity patterns along a desert riparian-upland gradient. PLoS One 7: e28235.
- Steward, A. L., J. C. Marshall, F. Sheldon, B. Harch, S. Choy, S. E. Bunn, and K. Tockner. 2011. Terrestrial invertebrates of dry river beds are not simply subsets of riparian assemblages. Aquat. Sci. 73: 551–566.
- Sun, R., X. Z. Yuan, and J. J. Ding. 2010. Plant communities in water-level-fluctuating-zone of Baijia Stream in Three Gorges Reservoir after its initiate impounding to 156 m height. Wetland Sci. 8: 1–7. (in Chinese)

- Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: present state and future trends. Environ. Conserv. 29: 308–330.
- Tong, X. X., C. D. Chen, S. J. Wu, Z. Y. Jia, X. M. Yi, and M. H. Ma. 2018. Spatial distribution pattern of plant community and habitat impact analysis of the drawdown zone of Pengxi River in the Three Gorges Reservoir. Acta Ecol. Sin. 38: 571–580. (in Chinese)
- Uetz, G. W., K. L. Van Der Laan, G. F. Summers, A. K. G. Patricia, and L. L. Getz. 1979. The effects of flooding on floodplain arthropod distribution, abundance and community structure. Am. Midl. Nat. 101: 286–299.
- Wang, Q., X. Yuan, J. H. Willison, Y. Zhang, and H. Liu. 2014. Diversity and above-ground biomass patterns of vascular flora induced by flooding in the drawdown area of China's Three Gorges Reservoir. PLoS One 9: e100889.
- Wang, K., X. Yuan, S. Wu, G. Zhang, H. Liu, L. Zhou, and M. Zhang. 2019. Effects of river damming on ground-dwelling arthropods along riparianupland habitats. Ecohydrology 12: e2073.
- Xiao, H., and J. Yue. 2016. Preliminary study of insects biodiversity on the drawdown zone litter-layer at Pengxi River in three gorges reservoir. Ecol Environ Monit Three Gorges 1: 58–64. (in Chinese)
- Yin, W. 1998. Pictorical keys to soil animals of China. Science Press, Beijing, China. (in Chinese)
- Yuan, F., Y. Zhang, J. Feng, and B. Hua. 2006. Taxonomy of Hexapoda, 2nd ed. China Agriculture Press, Beijing, China. (in Chinese)
- Yuen, E. Y., and D. Dudgeon. 2015. Spatio-temporal variability in the distribution of ground-dwelling riparian spiders and their potential role in waterto-land energy transfer along Hong Kong forest streams. PeerJ 3: e1134.