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Variation in species assemblages due to micro-topography and flow regime govern vegetation carbon stock in seasonal floodplain wetlands

Priyanka Sarkar¹, Tapati Das^{1*} and Dibyendu Adhikari²

Abstract

Hypothesis: Variation in species assemblages due to micro-topographic features and flow regime determine vegetation carbon stock in floodplain wetlands.

Material and method: We tested this hypothesis in Chatla—a tropical floodplain wetland located in northeast India. Five sampling stations characterized by contrasting micro-topographic and flow parameters were selected in the wetland for study. Species composition, assemblage pattern, and vegetation carbon stock were studied in these stations during three flood phases, i.e., early, middle, and late flood phases following standard methods. Univariate and multivariate statistics were used to determine the relationship between the selected environmental parameters, plant species assemblages, and vegetation carbon stock of the wetland.

Results: Thirty-one species of herbs and five species of shrubs were recorded from the five stations in Chatla floodplain wetland. Flow regime characterized by water flow velocity and discharge showed substantial variations across the stations. These parameters in turn are related to variations in the micro-topographic characteristics namely depth, width, and cross-sectional area of the stations. Plant species composition and abundance differed significantly with respect to micro-topography and flow regime as revealed by the cluster diagram. The canonical correspondence analysis revealed strong association of plant species assemblages with the micro-topography and flow regime within the wetland. Multiple regression analysis revealed a significant positive relationship of the vegetation carbon stock with the water discharge.

Conclusions: Spatial variation in plant species diversity because of micro-topography and flow regime determines the vegetation carbon stock in floodplain wetlands. Modification of these parameters by anthropogenic activities such as mining and quarrying may potentially influence the carbon stocking potential of seasonal floodplain wetlands. Therefore, appropriate measures should be taken to maintain the integrity of the natural topographic features of such wetlands.

Keywords: Riparian vegetation, Tropical wetland, Vegetation biomass, Ecosystem services, Northeast India

* Correspondence: dr.tapatidas@gmail.com

¹Department of Ecology and Environmental Science, Assam University, Silchar 788011, India

Full list of author information is available at the end of the article

Introduction

Tropical floodplain wetlands provide numerous ecological services through regulation of hydrological cycle, facilitation of groundwater recharge, controlling flood risk by modifying the river discharge, and support diverse livelihood activities (Costanza et al. 1997; Tockner and Stanford 2002; Murphy et al. 2003; Mitsch and Gosselink 2015). They are also one of the most carbon-rich ecosystems storing ~ 250 Gt of carbon (Neue et al. 1997; Bernal and Mitsch 2013; Kolka et al. 2016). Particularly, seasonal floodplain wetlands act as a significant carbon sink by sequestering vast amounts of organic carbon in soil and vegetation ranging from 69.2 to 114.3 g C m⁻² year⁻¹, that could help in mitigating the impact of climate change (Walling et al. 2006; Cierjacks et al. 2010; Sutfin et al. 2016; Craft et al. 2018).

The carbon stocking capacity of wetlands is modulated by various environmental factors such as climate, hydrology, soil, vegetation, land conversion, and management practices (Adame et al. 2015; Kolka et al. 2016; Watkins et al. 2017). The effect of these factors may be understood at various spatial, e.g., local, regional, and global, and temporal frames of reference, e.g., ten to hundreds of years (Carnell et al. 2018). Nevertheless, to design and implement effective management strategies, it is necessary to understand how the proximal abiotic factors influence the pattern and mechanism of carbon stocking in tropical wetlands (Mitra et al. 2005; Kolka et al. 2016).

Unplanned urbanization and infrastructure development resulting in modification of micro-topography and flow threaten the integrity of freshwater ecosystems thereby disrupting the provisioning and regulating services (Kumar et al. 2008; Zhao et al. 2006; Bassi et al. 2014). It is important to understand the mechanism, as to how variation in the micro-topographic settings may affect the aquatic ecosystem structure and function. Topographic features and water flow regime are arguably among the key factors influencing wetland ecosystem functioning (Adhikari et al. 2009; McLaughlin and Cohen 2013). Especially in floodplain wetlands, the fluvial action of flooding under a particular set of basin structure creates a mosaic of habitat patches across the landscape (Ward et al. 1999). Here, some species may be restricted to permanently flooded stagnant wetlands, while the others are found in the areas experiencing fluctuating hydroperiods (Conner and Day Jr 1982; Cherry 2011). Nonetheless, plant assemblages are also strongly influenced by the topographic variations in the aquatic ecosystems, which are the result of the incoming water and sediment regimes in the fluvial system (Bendix and Hupp 2000). Such variation in the topography creates a depth gradient to which the aquatic plants exhibit various physiological adaptations (Lacoul and Freedman 2006). Thus, the environmental factors such as micro-topographic settings and flow variation

profoundly influence the structure and function of the wetland ecosystems by affecting species richness, diversity, productivity, organic matter accumulation, and nutrient cycling (Bendix and Hupp 2000; Van Der Valk 2005; Elozegi et al. 2010; McLaughlin and Cohen 2013).

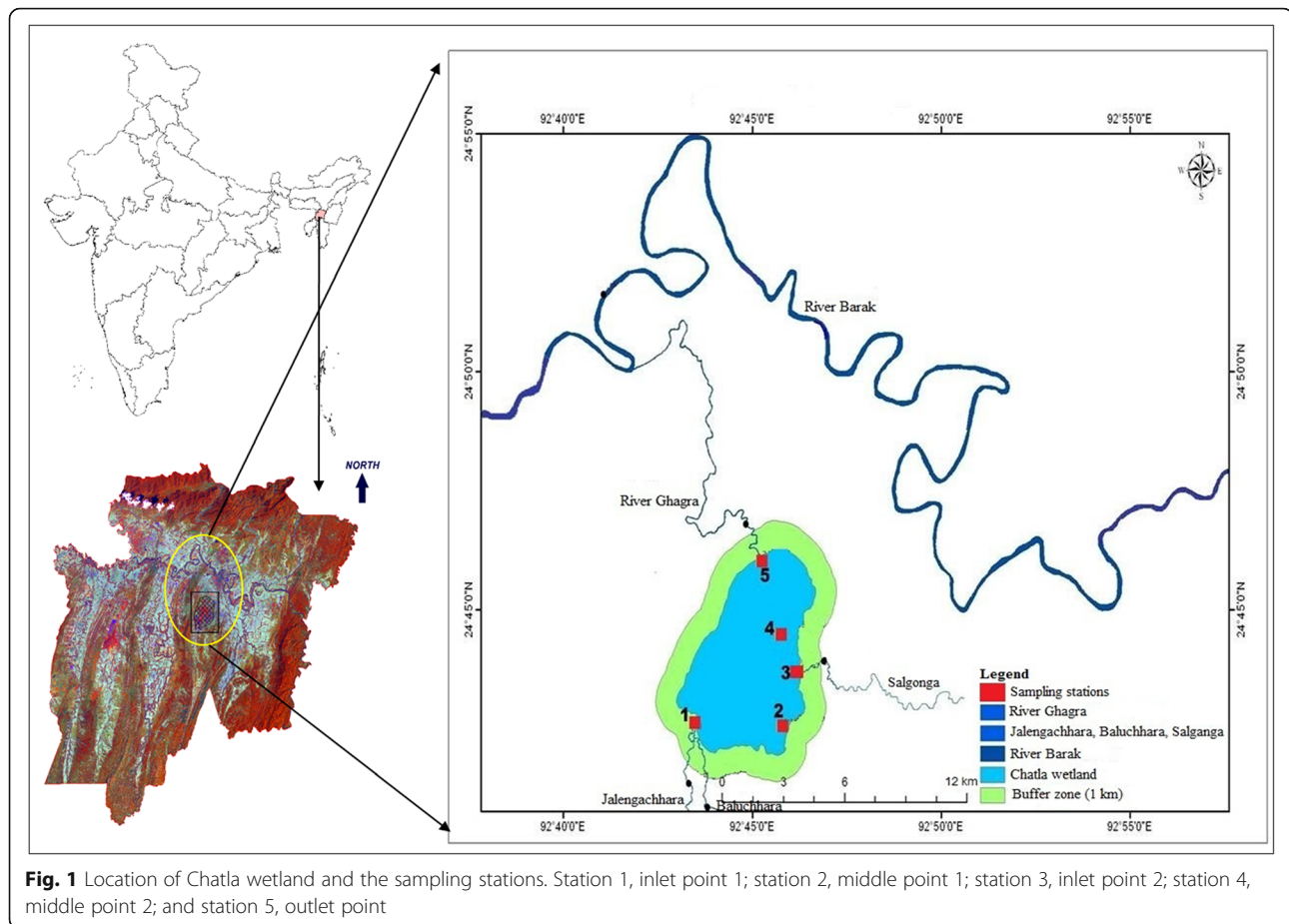
In the present study, we hypothesized that variation in the plant species assemblages due to different micro-topographic and water flow regime should influence the vegetation carbon stock in tropical floodplain wetlands. We tested this hypothesis in Chatla—a tropical seasonal floodplain wetland in the Barak river basin of Assam in Northeast India. The aims of our study were to investigate whether (1) differences in the wetland micro-topography and flow regime cause heterogeneous environmental conditions, (2) the environmental heterogeneity influences plant species assemblage and abundance patterns, and (3) all of these factors influence the vegetation carbon stock in the wetland.

Materials and methods

Study area

We have undertaken the present study in Chatla—a seasonal floodplain wetland located in Cachar district of the state of Assam in northeast India (Fig. 1). The wetland is a part of the Barak river system, and retains water during pre-monsoon to post-monsoon periods, i.e., from April to October; and, experiences a dry phase mostly during the winter to early phase of pre-monsoon, i.e., from November to March (Fig. 2). The topography of Chatla is characterized by low-lying areas covering an area of ~ 10 km² with mosaics of numerous small hillocks. The primary inlet points of Chatla comprise of streams namely Jalengachhara, Baluchhara, and Salganga, among which the streams Jalengachhara and Baluchhara confluence before entering Chatla (Kar et al. 2008). The only outlet point is river Ghagra—a tributary of river Barak (Kar et al. 2008) which is a part of the Surma-Meghna river system in the Indian subcontinent. As the fluvial pattern in seasonally inundated Chatla changes with a change in seasonal rainfall, the study was carried out during the flood, when the entire wetland was inundated and turned into a continuous system.

Considering the spatiotemporal variations in micro-topography and water flow regime in Chatla, five sampling stations comprising of two inlet points (stations 1 and 3), two middle points (stations 3 and 4), and one outlet point (station 5) were selected in the wetland (Fig. 1). In each sampling station, measurements of wetland micro-topography and sampling of wetland vegetation were done during each flood stage namely early flood phase (EFP; May to June), mid-flood phase (MFP; July to



August), and late flood phase (LFP; September to October) during years 2014 and 2015 (Fig. 3).

Micro-topographic features and water flow regime

The micro-topographic features of the wetland examined were depth, width, and cross-sectional area. Also, the flow regime examined in this study includes average water velocity and water discharge. During each sampling period, the depth measurements ($n = 5$) in each sampling stations were done using a measuring pole while the width in the inlet ($n = 5$) and outlet points ($n = 5$) was measured using a measuring tape. The widths in the middle points of the wetland at 2 locations were measured using the line ruler tool of Google earth pro software version by plotting the respective GPS coordinates for the months of June, August, October for 2014 and 2015.

Cross-sectional area in each of the sampling station was calculated by multiplying the corresponding depth and width values of the respective sampling stations (Karume et al. 2016). All the micro-topographic and flow parameters were measured several times ($n = 5$) in each sampling stations during each flood phase. Average

water velocity and water discharge at the inlets and outlet point where lotic condition prevailed during the flood phases were determined following the float method (Gordon et al. 2004) using the equations below.

$$\text{Average water velocity (m s}^{-1}\text{)} = \frac{L}{t} \times k \dots \quad (1)$$

where L is the distance (m) traveled by the float in time t (s) and k is the bed roughness coefficient (0.85)

$$\text{Water discharge (cubic m s}^{-1}\text{)} = VA \dots \dots \dots \quad (2)$$

where V is the average water velocity (m s^{-1}) and A is the cross-sectional area (m^2).

Sampling and analysis of wetland vegetation

We studied the species composition, diversity, and community characteristics of the lower angiosperm groups of the riparian vegetation by laying ten random quadrats of 1×1 m size along the riparian zone of each sampling station during each flood phases for two consecutive years. Overall, 300 quadrats were sampled during the entire survey period. Plant species were identified using

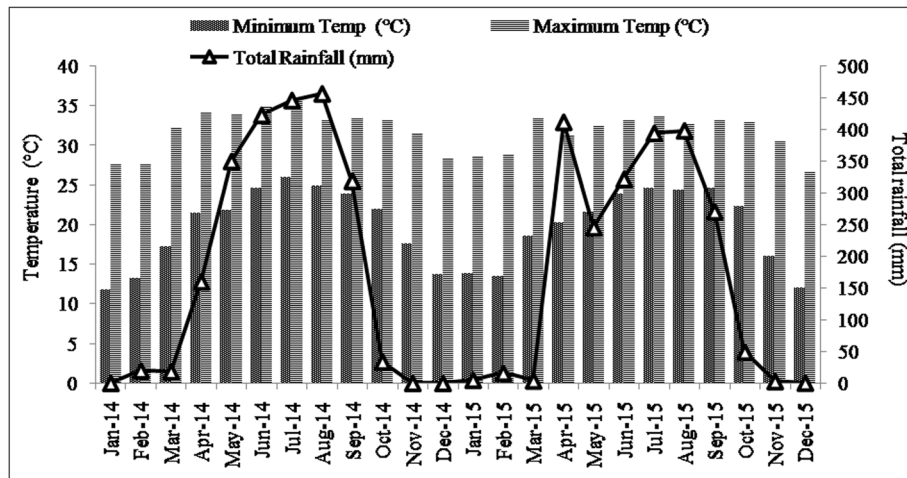


Fig. 2 Monthly variations in total rainfall and atmospheric temperature in Cachar district during study period (2014–2015). The study was carried out during early-flood phase (EFP; May to June), mid-flood phase (MFP; July to August) and late flood phase (LFP; September to October)

regional floras of Kanjilal et al. (Kanjilal et al. 1934, 1936, 1938, 1940), online database www.theplantlist.org, and the herbaria of the Botanical Survey of India (BSI), Shillong. The community characteristics such as frequency, density, basal area, relative frequency, relative density, relative basal area, and importance value index (IVI, a measure of the dominance of a species) were determined following standard methods (Kent 2011).

Plant species richness and diversity indices for the sampling stations were calculated using Shannon-Wiener diversity index (Shannon and Wiener 1963), Simpson dominance index (Simpson 1949), and Buzas and Gibson's Evenness index (Buzas and Gibson 1969). Taxonomic distinctness was determined using three levels of taxonomic

information such as species, genus, and family (Warwick and Clarke 1995; Clarke and Warwick 1998). Cluster analysis using Euclidean distance was also done to identify the similarity and dissimilarity in the assemblage of the wetland vegetation across the selected sampling stations (Krebs 1989). Computation of all the abovementioned parameters of the wetland vegetation was performed using PAST software (version 3.22) (Hammer 2011).

Biomass and carbon stock estimation of wetland vegetation

Above- and below-ground biomass and carbon stock of the wetland vegetation was estimated using representative plant samples collected from three random quadrats of 1

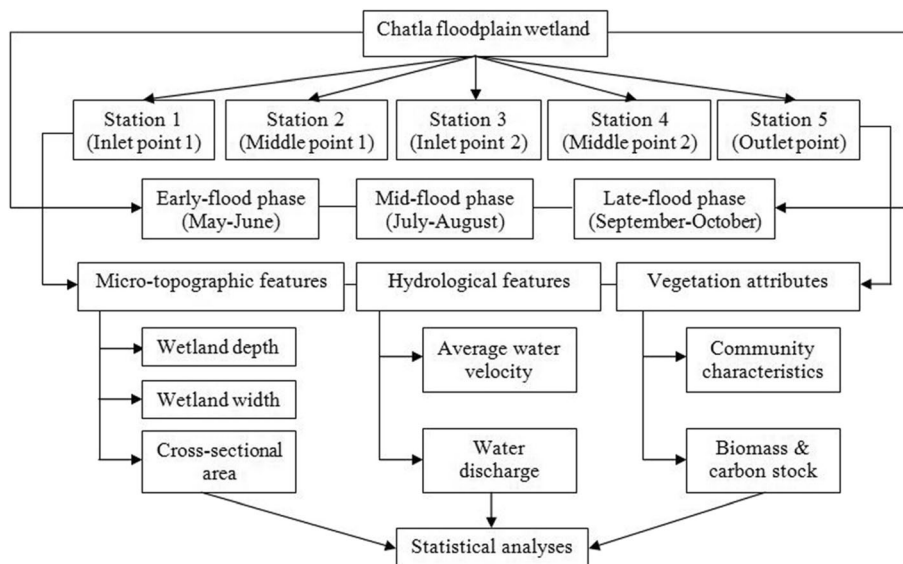


Fig. 3 Methodological framework of the present study

× 1 m size laid in each sampling station during each flood phase for 2 years (Misra 1968). Overall, we sampled 90 quadrats during the entire study period. To minimize loss of below-ground plant parts, we excavated soil monoliths while uprooting the plant samples from each quadrat (Van der Maarel and Titlyanova 1989) in the littoral zone (within the partially submerged area to 2 m from the shoreline) in each sampling station. Subsequently, the plant samples were brought to the laboratory and washed with distilled water. The samples were segregated and labeled species-wise, and oven-dried at a temperature of 70 °C for 48 h. The oven-dried samples were weighed using an electronic balance to determine the biomass of the individual plant species. We determined the total biomass of each species through the summation of the above-ground and below-ground biomass of the individuals of the respective species. For estimation of the carbon stock of the individual plant species, the corresponding biomass values of each species were multiplied with a conversion factor of 0.45 (Woomer 1999). The carbon stock values (g m^{-2}) of the recorded plant species were multiplied by a factor of 0.01 to convert into Megagram per hectare (Mg ha^{-1}). The total carbon stock (Mg ha^{-1}) of the wetland vegetation for each station was estimated by summing up the carbon stock (Mg ha^{-1}) values of all the plant species present in the respective stations.

Statistical analysis

Shapiro-Wilk test was done to check the normality of the data. One-way analysis of variance (ANOVA) was performed for normally distributed data while a Kruskal-Wallis test was performed for non-normal data. ANOVA was performed to test the statistical significance of the variations in micro-topographic attributes such as depth, width, and cross-sectional area; flow parameters such as average water velocity and water discharge, and vegetation characters such as species richness, diversity indices, taxonomic distinctness and carbon stock of the wetland vegetation in different sampling stations and among the flood phases of the wetland. Tukey post-hoc analyses were performed to identify the dominant micro-topographic attributes, water flow regime, and vegetation characters that created variations across different sampling stations. Kruskal-Wallis test was performed to assess the statistical significance of the variations in non-normal variables such as density, IVI, and carbon stock of different species of wetland vegetation across different sampling stations. Multiple regression analysis was performed to study the effect of wetland micro-topography and water flow regime on vegetation carbon stock. All the statistical analyses were performed using SPSS software (version 20) (Nie et al. 2011). Canonical correspondence analysis (CCA) was performed to study the relationship between the plant species assemblages with

micro-topographic conditions and water flow regime in the wetland using CANOCO software (version 4.5, Trial version) (Ter Braak and Smilauer 2002).

Results

Species composition and diversity

Overall, we recorded 36 species of lower groups of angiosperms comprising of 31 herbs and 5 shrubs, belonging to 16 families from the study area (Table 1). Poaceae represented by 14 species was the dominant family, followed by Cyperaceae with six species. Herbaceous species were more than shrubs across all the stations. However, when compared, the number of herbaceous species was higher in the inlet and outlet points compared to the middle points, and the reverse trend was observed for the shrubs. Overall family and species richness of wetland vegetation were higher in the inlet and outlet points as compared to the middle points (Table 1). However, the species richness did not vary significantly among the stations (Table 2).

On average, the Shannon-Wiener diversity index and Buzas & Gibson's Evenness index were significantly higher in inlet and outlet points compared to the middle points, while the Simpson dominance index was significantly higher in middle points compared to other sites (Tables 1 and 2). One-way ANOVA revealed significant variations in all diversity indices across the sampling stations (Table 2). Tukey HSD post-hoc multiple comparisons test revealed significant differences in the mean values of Simpson dominance index and Buzas and Gibson's evenness index were between the station pair 2–3, while significant differences in the mean values of Shannon-Wiener diversity index were observed between station pairs 2–3 and 2–4 (Table 3). The density of the Poaceae members was highest in all the stations and particularly in the inlet and outlet points. Following Poaceae, the density of Cyperaceae members was comparatively higher in the middle points (Additional file 1: Table S1). The average taxonomic distinctness of wetland vegetation was higher in the middle points as compared to the inlets and outlet points (Fig. 4a), though one-way ANOVA did not reveal significant differences in taxonomic distinctness among the stations (2). Cluster analyses of the wetland vegetation revealed two distinct groups, of which, one group comprised of vegetation across the inlet and outlet points of the wetland, while the other group comprised of vegetation across the middle points (Fig. 4b).

Species richness was significantly higher during the mid-flood phase and lowest during the late flood phase (Additional file 2: Figure S1a and Additional file 1: Table S2). Species diversity index was significantly higher during the early flood phase and lowest during the late flood phase (Additional file 2: Figure S1b, and Additional file

Table 1 Distribution and diversity profile of vegetation in the wetland across different sampling stations

Family and taxa	Station 1 (Inlet point 1)	Station 2 (Middle point 1)	Station 3 (Inlet point 2)	Station 4 (Middle point 2)	Station 5 (Outlet point)
Amarathaceae					
<i>Alternanthera paronychioides</i> A. St.-Hil	-	-	+	-	+
<i>Alternanthera sessilis</i> (L.) R. Br.ex DC.	+	-	+	-	+
Apiaceae					
<i>Centella asiatica</i> (L.) Urb.	+	+	+	+	+
Compositae					
<i>Centipeda minima</i> (L.) A. Braun & Asch.	-	-	-	-	+
<i>Eclipta prostrata</i> (L.) L.	-	-	+	-	+
Araceae					
<i>Colocasia esculenta</i> (L.) Schott	+	-	-	-	-
Arecaceae					
<i>Calamustenuis</i> Roxb.	-	-	-	+	-
Ceratophyllaceae					
<i>Ceratophyllum demersum</i> L.	-	+	-	-	-
Convolvulaceae					
<i>Ipomoea carnea</i> Jacq.	+	+	+	-	+
Cyperaceae					
<i>Cyperus haspan</i> L.	-	+	-	-	-
<i>Cyperus javanicus</i> Houltt.	-	+	-	-	-
<i>Cyperus compressus</i> L.	-	-	+	-	+
<i>Eleocharis acicularis</i> (L.) Roem. & Schult.	-	-	-	+	-
<i>Fimbristylis bisumbellata</i> (Forssk.) Bubani	-	+	-	+	+
<i>Fimbristylis littoralis</i> Gaudich.	+	-	-	-	-
Euphorbiaceae					
<i>Croton bonplandianus</i> Baill.	-	-	-	+	-
Marantaceae					
<i>Schumannianthus dichotomus</i> (Roxb.) Gagnep.	-	+	-	-	-
Melastomataceae					
<i>Melastoma malabathricum</i> L.	-	+	-	-	-
Onagraceae					
<i>Ludwigia hyssopifolia</i> (G.Don) Exell	-	-	+	-	-
Poaceae					
<i>Axonopus fissifolius</i> (Raddi) Kuhlms.	-	-	-	+	-
<i>Brachiaria ramosa</i> (L.) Stapf	+	-	+	-	-
<i>Chrysopogon aciculatus</i> (Retz.) Trin.	+	-	+	+	-
<i>Chrysopogon zizanioides</i> (L.) Roberty	+	+	+	+	+
<i>Cynodon dactylon</i> (L.) Pers.	+	+	+	+	+
<i>Digitaria ciliaris</i> (Retz.) Koeler	-	-	-	-	+
<i>Eleusine indica</i> (L.) Gaertn.	+	-	-	-	-
<i>Eragrostis uniolooides</i> (Retz.) Nees ex Steud.	+	-	-	-	-
<i>Hemarthria compressa</i> (L.f.) R.Br.	-	-	+	-	-
<i>Paspalum notatum</i> Flüggé	+	-	-	-	+
<i>Paspalum scrobiculatum</i> L.	-	+	-	-	-

Table 1 Distribution and diversity profile of vegetation in the wetland across different sampling stations (*Continued*)

Family and taxa	Station 1 (Inlet point 1)	Station 2 (Middle point 1)	Station 3 (Inlet point 2)	Station 4 (Middle point 2)	Station 5 (Outlet point)
<i>Pseudoraphis spinescens</i> (R.Br.) Vickery	-	+	+	-	-
<i>Saccharum ravennae</i> (L.) L.	-	+	+	-	+
<i>Sacciolepis interrupta</i> (Willd.) Stapf	+	-	-	-	-
Polygonaceae					
<i>Panicum polyanthemum</i> (L.) Delarbre	+	-	+	-	+
Pontederiaceae					
<i>Eichhornia crassipes</i> (Mart.) Solms	+	-	+	+	+
Rubiaceae					
<i>Oldenlandia diffusa</i> (Willd.) Roxb.	-	+	+	+	+
Total family: 16	Family (8)	Family (8)	Family (10)	Family (7)	Family (8)
Total taxa: 36	Taxa (15)	Taxa (14)	Taxa (17)	Taxa (11)	Taxa (16)
	Herb (14)	Herb (11)	Herb (16)Shrub (1)	Herb (9)	Herb (15)
	Shrub (1)	Shrub (3)		Shrub (2)	Shrub (1)
Shannon-Wiener Diversity index	1.14	1.18	0.68	0.65	1.08
	±0.50	±0.06	±0.38	±0.44	±0.37
	(0.49-1.56)	(1.12-1.25)	(0.22-1.23)	(0.13-1.16)	(0.73-1.53)
Simpson Dominance index	0.48	0.36	0.63	0.65	0.41
	±0.27	±0.02	±0.19	±0.26	±0.13
	(0.26-0.91)	(0.33-0.39)	(0.36-0.90)	(0.34-0.95)	(0.25-0.55)
Buzas and Gibson's Evenness index	0.54	0.51	0.40	0.45	0.53
	±0.07	±0.06	±0.03	±0.17	±0.11
	(0.41-0.60)	(0.43-0.59)	(0.35-0.43)	(0.20-0.71)	(0.41-0.70)

"-" represents an absence of the taxa concerned; total number of quadrats studied = 300; for diversity indices mean ± SD, $n = 6$; values within parenthesis represent the range of the respective mean value

1: Table S2). However, the dominance and evenness indices and taxonomic distinctness did not vary significantly across the flood phases (Additional file 2: Figure S1c–e and Additional file 1: Table S2). The dominance–diversity curve of the wetland vegetation revealed that during the flood phase, most of the resources of wetland were shared among few dominant species (Additional file 2: Figure S2), with *Chrysopogon*

Table 2 One-way analyses of variance showing variations in vegetation attributes in the wetland with sampling stations as the main effect variable

Parameters	<i>F</i> -statistic
Species richness	1.113 ^{ns}
Diversity indices	
Simpson dominance index	3.684*
Shannon-Wiener diversity index	3.295*
Buzas and Gibson's evenness index	3.137*
Taxonomic distinctness	2.685 ^{ns}
Total C stock (Mg ha ⁻¹)	0.962 ^{ns}

Degree of freedom ($n - 1$) = 4; *ns* non-significant

** $p < 0.01$

* $p < 0.05$

zizanioides being the most dominant species in all the sampling stations (Additional file 1: Tables S3, S4).

Spatial and temporal variations in micro-topography and water flow regime

Depth was more in the inlet and outlet points of the wetland as compared to its middle points (Table 4). The wetland width and cross-sectional area were higher in the middle points as compared to the inlet and outlet points. One-way ANOVA revealed significant variations in the micro-topographic variables, namely, width, and cross-sectional area across the sampling stations (Table 4). Tukey HSD post-hoc multiple comparison test revealed significant differences in the mean width between the station pairs 1–2, 1–4, 2–3, 2–5, 3–4, and 4–5 (Table 4). Similarly, significant differences in the cross-sectional area were observed between the station pairs 1–4, 3–4, and 4–5 (Table 4). The average water velocity and discharge were higher in the inlet and outlet points, whereas the values were very low (below detectable level) in the middle points (Table 4). One-way ANOVA revealed significant differences in the

Table 3 Multiple comparisons of vegetation attributes in the wetland at different sampling stations using Tukey Post-hoc analysis

Parameters	Station (I)	Station (J)	Mean difference (I - J)	
Vegetation attributes	Simpson dominance index	Station 1	Station 2	0.17243 ^{ns}
		Station 3	-0.19695 ^{ns}	
		Station 4	-0.16725 ^{ns}	
		Station 5	0.07802 ^{ns}	
		Station 2	Station 3	-0.36938*
	Station 4	-0.33968 ^{ns}		
	Station 5	-0.09442 ^{ns}		
	Station 3	Station 4	0.02970 ^{ns}	
	Station 5	0.27497 ^{ns}		
	Shannon-Wiener diversity index	Station 4	Station 5	0.24527 ^{ns}
		Station 1	Station 2	-0.33268 ^{ns}
		Station 3	0.37373 ^{ns}	
		Station 4	0.40460 ^{ns}	
		Station 5	-0.03017 ^{ns}	
		Station 2	Station 3	0.70642*
Station 4		0.73728*		
Station 5		0.30252 ^{ns}		
Station 3		Station 4	0.03087 ^{ns}	
Station 5		-0.40390 ^{ns}		
Buzas and Gibson's evenness index	Station 1	Station 2	-0.02285 ^{ns}	
	Station 3	0.18023 ^{ns}		
	Station 4	0.06898 ^{ns}		
	Station 5	-0.01743 ^{ns}		
	Station 2	Station 3	0.20308*	
	Station 4	0.09183 ^{ns}		
	Station 5	0.00542 ^{ns}		
	Station 3	Station 4	-0.11125 ^{ns}	
	Station 5	-0.19767 ^{ns}		
	Station 4	Station 5	-0.08642 ^{ns}	

Station 1 = inlet point 1; station 2 = middle point 2; station 3 = inlet point 2; station 4 = middle point 2; station 5 = outlet point; degree of freedom ($n - 1$) = 4

^{ns}Non-significant

* $p < 0.05$

** $p < 0.01$

water flow regime, namely water velocity and discharge among the sampling stations (Table 4). Tukey HSD post-hoc comparisons test revealed significant differences in the mean values of water velocity and water discharge between the station pairs 1–2, 1–4, 2–3, and 3–4 (Table 5).

Depth, width, cross-sectional area, and water discharge were highest during the mid-flood phase, while water velocity was highest during the early flood phase (Additional

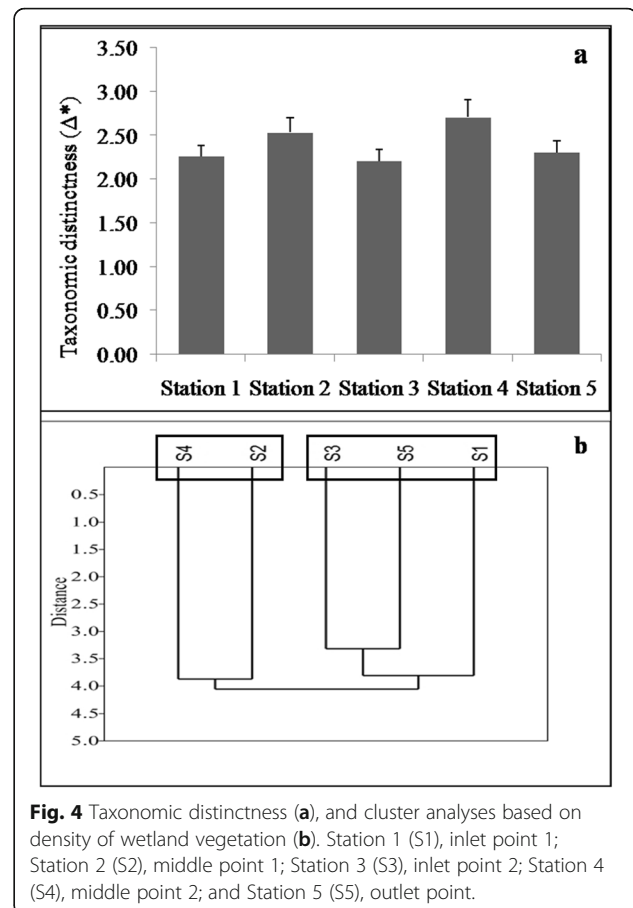


Fig. 4 Taxonomic distinctness (a), and cluster analyses based on density of wetland vegetation (b). Station 1 (S1), inlet point 1; Station 2 (S2), middle point 1; Station 3 (S3), inlet point 2; Station 4 (S4), middle point 2; and Station 5 (S5), outlet point.

file 2: Figure S3a–S3e). Depth and water discharge were lowest during the late flood phase, while width and cross-sectional area were lowest during the early flood phase. Only the water velocity was observed to be lowest during the mid-flood phase (Additional file 2: Figure S3d). The differences in the various parameters between various flood phases were statistically non-significant (Additional file 1: Table S2).

Relationship of species assemblage with wetland micro-topography and water flow regime

The CCA ordination plot revealed that most of the plant species assemblages were strongly associated with the micro-topography and water flow regime within the wetland (Fig. 5 and Table 6). The ordination plot revealed that species such as *Brachiaria ramosa*, *Centella asiatica*, and *Colocasia esculenta* were associated with depth, while *Alternanthera paronychioides*, *Persicaria hydropiper*, and *Hemarthria compressa* were associated with water velocity. *Alternanthera sessilis*, *Digitaria ciliaris*, and *Eragrostis unioides* were associated with water discharge; *Axonopus fissifolius*, *Eleocharis acicularis*, and *Calamus tenuis* were associated with cross-sectional area, and *Croton bonplandianus* was associated with

Table 4 Micro-topography and flow parameters in the wetland in different sampling stations; and, one-way analyses of variance showing variations in micro-topography and flow parameters in the wetland with sampling stations as the main effect variable

Parameters	Station 1 (inlet point 1)	Station 2 (middle point 1)	Station 3 (inlet point 2)	Station 4 (middle point 2)	Station 5 (outlet point)	F-statistic
Depth (m)	0.84 ± 0.67 (0.35–2.25)	0.47 ± 0.11 (0.30–0.68)	1.09 ± 0.53 (0.50–2.20)	0.71 ± 0.26 (0.30–1.54)	0.64 ± 0.16 (0.32–0.79)	2.556 ^{ns}
Width (m)	25.14 ± 12.16 (12–52)	1217.50 ± 1387.42 (65–4050)	13.31 ± 6.27 (8–25)	1720 ± 512.69 (950–2500)	20 ± 8.87 (10–38)	8.024**
Cross-sectional area (m ²)	27.55 ± 35.78 (4.92–117)	583.82 ± 499.04 (94.11–1091.71)	17.12 ± 17.41 (6.89–37.23)	1188.54 ± 276.39 (962.15–1496.55)	13.30 ± 7.60 (5.33–20.50)	10.076**
Water velocity (m s ⁻¹)	0.34 ± 0.22 (0.05–0.76)	BDL	0.32 ± 0.21 (0.10–0.72)	BDL	0.19 ± 0.07 (0.10–0.30)	7.369**
Water discharge (Cubic m s ⁻¹)	4.87 ± 2.98 (1.23–13.64)	BDL	4.34 ± 3.40 (0.52–11.25)	BDL	2.56 ± 1.60 (0.45–4.74)	7.369**

Mean ± SD; n = 6; values within parenthesis represent the range of the respective mean value; BDL Below detectable limit; for F-statistic, degree of freedom (n – 1) = 4

**p < 0.01

*p < 0.05

width (Fig. 5 and Table 6). Furthermore, species such as *Cynodon dactylon*, *Eichhornia crassipes*, *Chrysopogon zizanioides* that occurred in the middle of the ordination plot acted as generalists species.

Effect of micro-topography and water flow regime on vegetation carbon stock

The average carbon stock in wetland vegetation was higher in inlet and outlet points as compared to the middle points (Fig. 6, and Additional file 1: Table S4), though the variation was not significantly different among the sampling stations (Table 3). Flood phase wise variations in the vegetation carbon stock revealed significantly higher carbon stock during the mid-flood phase and lowest during the late flood phase (Additional file 2: Figure S4, and Additional file 1: Table S2). The multiple regression analysis for vegetation carbon stock against the micro-topographic and water flow regimes of wetland revealed a significant positive relationship of the vegetation carbon stock with the water discharge (Table 7, and Additional file 1: Table S5 and S6).

Discussion

Studying the relationship between topography and flow variation in wetlands is important as it has profound implications on its ecological functionality (Håkanson 1981; Sperling 1999; Nöges 2009; Stefanidis and Papastergiadou 2012). The present study revealed substantial variations in the water flow regime characterized by average water velocity and discharge across the sampling stations. We attribute these to the variations in the wetland micro-topographic characteristics such as depth, width, and cross-sectional area in the sampling stations across the wetland. Several other studies have also inferred that the topographic characteristics of aquatic ecosystems are among the significant determinants of flow variation (Wetzel 2001; Camila

de Sousa et al. 2011; Yunus et al. 2003; Singh et al. 2014; Pandi et al. 2017; Soni 2017; Prabhakaran and Raj 2018), which in turn create heterogeneous micro-environments within wetlands.

Habitat heterogeneity created due to varying topographic and hydrologic characteristics generally determine the growth and distribution of aquatic vegetation (Ward et al. 1999; Bendix and Hupp 2000; Van Der Valk 2005; Camporeale and Ridolfi 2006). Such variations facilitate the plant species to colonize, co-exist, and proliferate (Dahlberg 2016; Larkin 2016; Schneider et al. 2018). This is evident in our study, where varying environmental condition putatively resulted in differential species assemblage pattern. For instance, the vegetation analysis revealed distinct species assemblage patterns in the stations with different micro-topographic parameters and water flow conditions. The CCA ordination plot revealed that species such as *Alternanthera paronychioides*, *Alternanthera sessilis*, *Brachiaria ramosa*, *Eclipta prostrata*, *Hemarthria compressa*, and *Persicaria hydropiper* were abundant in the inlet and outlet points of the wetland, which had greater depth. On the other hand, species such as *Calamus tenuis*, *Ceratophyllum demersum*, *Eleocharis acicularis*, *Melastoma malabathricum*, *Pseudoraphis spinescens*, and *Schumannianthus dichotomus* were abundant in the middle points which had greater cross-sectional area. However, species such as *Chrysopogon aciculatus*, *Chrysopogon zizanioides*, *Cynodon dactylon*, *Fimbristylis bisumbellata*, *Ipomoea carnea*, and *Saccharum ravennae* were recorded in inlet, middle, and outlet points with varying micro-topographic attributes, and water flow regime.

The effect of habitat-related factors on species assemblage pattern is also reflected in the cluster diagram where the vegetation across the inlet and outlet points formed one cluster, while those across the middle points

Table 5 Multiple comparisons of the micro-topography, and flow parameters in the wetland at different sampling stations using Tukey Post-hoc analysis

Parameters		Station (I)	Station (J)	Mean difference (I – J)
Micro-topography	Width (m)	Station 1	Station 2	– 1192.36*
			Station 3	11.83 ^{ns}
			Station 4	– 1694.86**
			Station 5	5.14 ^{ns}
		Station 2	Station 3	1204.19*
			Station 4	– 502.49 ^{ns}
			Station 5	1197.50*
			Station 3	– 1706.69**
	Cross-sectional area (m ²)	Station 4	Station 5	– 6.69 ^{ns}
			Station 5	1699.99**
			Station 1	– 559.36 ^{ns}
			Station 2	2.49 ^{ns}
		Station 1	Station 3	– 1163.91**
			Station 4	– 9.83 ^{ns}
			Station 5	561.86 ^{ns}
			Station 2	– 604.55 ^{ns}
Water flow regime	Water velocity (m s ⁻¹)	Station 2	Station 3	549.53 ^{ns}
			Station 4	– 1166.41**
			Station 5	– 12.33 ^{ns}
			Station 3	– 1166.41**
		Station 3	Station 4	– 12.33 ^{ns}
			Station 5	1154.09**
			Station 1	0.33833*
			Station 2	0.01500 ^{ns}
	Water discharge (Cubic m s ⁻¹)	Station 4	Station 3	0.33833*
			Station 4	0.15000 ^{ns}
			Station 5	0.15000 ^{ns}
			Station 2	– 0.32333*
		Station 1	Station 3	0.00000 ^{ns}
			Station 4	– 0.18833 ^{ns}
			Station 5	– 0.18833 ^{ns}
			Station 2	0.32333*
Water discharge (Cubic m s ⁻¹)	Station 3	Station 4	0.13500 ^{ns}	
		Station 5	0.13500 ^{ns}	
		Station 1	– 0.18833 ^{ns}	
		Station 2	– 0.18833 ^{ns}	
	Station 4	Station 3	4.87168*	
		Station 4	0.52857 ^{ns}	
		Station 5	4.87168*	
		Station 2	2.31704 ^{ns}	
Station 2	Station 3	– 4.34311*		
	Station 4	0.00000 ^{ns}		
	Station 5	– 2.55463 ^{ns}		
	Station 3	– 2.55463 ^{ns}		
Station 3	Station 4	4.34311*		
	Station 5	1.78847 ^{ns}		
	Station 1	4.34311*		
	Station 2	1.78847 ^{ns}		
Station 4	Station 3	– 2.55463 ^{ns}		
	Station 4	– 2.55463 ^{ns}		
	Station 5	– 2.55463 ^{ns}		
	Station 2	– 2.55463 ^{ns}		

Station 1 = inlet point 1, station 2 = middle point 2, station 3 = inlet point 2, station 4 = middle point 2; station 5 = outlet point, degree of freedom ($n - 1$) = 4; *ns* = non-significant

* $p < 0.05$

** $p < 0.01$

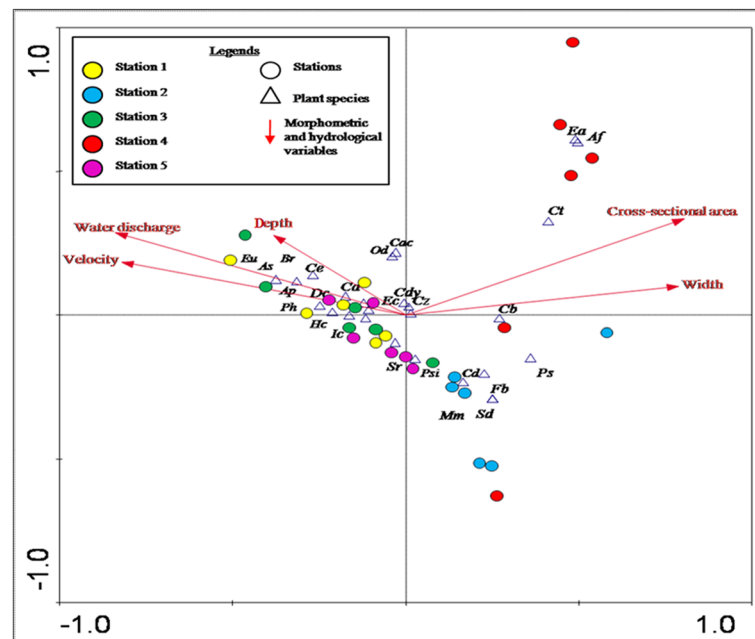


Fig. 5 Ordination plot of CCA elucidating the influence of micro-topography and flow regime on species assemblages. Abbreviations: Af *Axonopus fissifolius*, Ap *Alternanthera paronychioides*, As *Alternanthera sessilis*, Br *Brachiaria ramosa*, Ca *Centella asiatica*, Cac *Chrysopogon aciculatus*, Cb *Croton bonplandianus*, Cd *Ceratophyllum demersum*, Cdy *Cynodon dactylon*, Ce *Colocasia esculenta*, Ct *Calamus tenuis*, Cz *Chrysopogon zizanioides*, Dc *Digitaria ciliaris*, Ea *Eleocharis acicularis*, Ec *Eichhornia crassipes*, Eu *Eragrostis unioides*, Fb *Fimbristylis bisumbellata*, Hc *Hemarthria compressa*, Ic *Ipomoea carnea*, Mm *Melastoma malabathricum*, Od *Oldenlandia diffusa*, Ph *Persicaria hydropiper*, Ps *Paspalum scrobiculatum*, Psi *Pseudoraphis spinescens*, Sd *Schumannianthus dichotomus*, Sr *Saccharum ravennae*

formed another cluster. The heterogeneous conditions in the inlet and outlet points due to greater water discharge and the associated change in the microhabitat condition in the presence of available resources from the tributaries plausibly allowed the maximum number of species to co-exist in those stations (Friedman and Auble 2000; Peralta et al. 2006). Consequently, the diversity of wetland plants was higher in inlet and outlet points of the wetland. On the other hand, lower diversity index of wetland vegetation in middle points can be attributed to limited resource due to low flow velocity and higher cross-sectional area, which facilitated only a few dominant species like *Chrysopogon zizanioides* and *Cynodon dactylon* to survive (Friedman and Auble 2000; Wright et al. 2015). However, no significant differences in species richness

among the sampling stations might be due to the high levels of disturbance that prevented occurrence of most species, preventing coexistence and reducing species richness (Sharpe and Baldwin 2009). On the other hand, flood phase wise, lowest species richness and diversity in the late flood phase of the wetland can be attributed to the increased nutrient loss and tissue damage of wetland vegetation due to increased disturbance as a result of increased flood fluctuation frequency (Bornette et al. 2008).

Plant species diversity and assemblage are intricately linked with various ecological processes like ecosystem productivity (Naeem et al. 1996; Hector et al. 1999), retention of nutrients (Ewel et al. 1991), ecosystem stability, and resilience (Tilman and Downing 1994; Tilman et al. 2006). Assemblages with richer functional groups enhance ecosystem functioning facilitated through species-specific traits (Balvanera et al. 2006; Sullivan et al. 2007). In the context of the present study, variation in the carbon stock of the wetland vegetation can be linked to species-specific traits such as leaf area index, leaf carbon concentration, higher root biomass (Rawat et al. 2015), and an extensive network of the root system (Chomchalow 2001; Lavania et al. 2016). All these result in rapid growth and high biomass accumulation, which influence ecosystem carbon input (Tang et al. 2018). As evident from our results, the diversity and assemblage of such species varied under varying water flow

Table 6 Results of canonical correspondence analysis (CCA) showing the strength of the species-environment relationship in the selected stations of the wetland

	Axis 1	Axis 2	Axis 3	Axis 4
Eigen values	0.358	0.281	0.167	0.08
Species-environment correlations	0.916	0.803	0.832	0.61
Cumulative percentage variance of species data	12.3	21.9	27.7	30.4
Cumulative percentage variance of species-environment relation	38.3	68.3	86.2	94.7

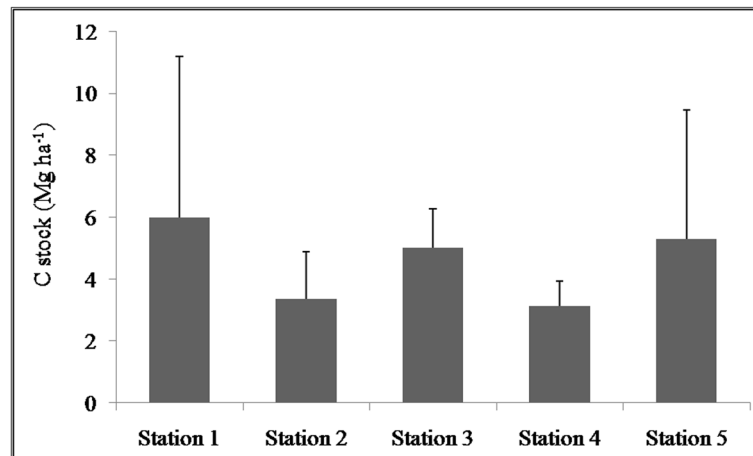


Fig. 6 Carbon stock (Mg ha^{-1}) of wetland vegetation across the different sampling stations namely station 1, inlet point 1; station 2, middle point 1; station 3, inlet point 2; station 4, middle point 2; and station 5, outlet point

regime and micro-topographic conditions. For example, species such as *Calamus tenuis*, *Schumannianthus dichotomus*, and *Melastoma malabathricum* growing abundantly in the middle points of the wetland have several adaptive traits such as greater plant height, higher leaf area and rate of seed production (Faravani and Bakar 2007), while the other species such as *Alternanthera sessilis*, *Eclipta prostrata*, *Hemarthria compressa*, and *Persicaria hydropiper* growing profusely in the inlet and outlet points have adaptive traits such as production of dense mats of extremely fine adventitious/superficial roots adapted for diverse range of moisture conditions that helped them in surviving under the given environmental conditions (Sultan 1995). The higher vegetation carbon stock in the inlet and outlet points compared to the middle points is, therefore, a result of the species adaptive response to the site-specific environmental condition.

Our study indicates that small-scale seasonal wetlands have the potential to mitigate the impact of climate change at a regional level by sequestering substantial amounts of carbon in the vegetation component. This is evident from our findings, which revealed that the vegetation stocked about $4.56 \text{ Mg C ha}^{-1}$ in the Chatla wetland, which is higher than the East Kolkata wetlands in India ($2.48 \text{ Mg C ha}^{-1}$, Pal et al. 2017). We have also elucidated

that the vegetation carbon stock in wetlands is influenced by the micro-topography and flow regime, which determines the species assemblage pattern in wetlands. Therefore, any change in the wetland micro-topography and flow regime within wetlands putatively lead to a shift in the plant species assemblage pattern within the wetland, thus upsetting the process of carbon sequestration. Currently, floodplain wetlands cover $\sim 6\%$ of the global land area, of which nearly 89% area is not protected (Reis et al. 2017). In Asia alone, $\sim 5000 \text{ km}^2$ of wetland area are lost annually due to anthropogenic factors such as agricultural expansion and dam construction (McAllister et al. 2001). Other factors leading to wetland degradation and loss around the world include urbanization, developmental activities, agricultural runoff, discharge of polluted industrial effluents, and climate change (Bassi et al. 2014). Such an unprecedented loss in the area of the wetlands may have a significant impact on their capacity to provide important ecological services that also include regulation of regional climate (Zedler and Kercher 2005).

Conclusion

We conclude that variations in micro-topographic factor like cross-sectional area and water flow regime like water velocity together govern the carbon stocking potential of the vegetation in seasonal floodplain wetlands. Thus, we

Table 7 Results of multiple regression analysis (using backward method) for carbon stock in wetland vegetation against the micro-topography and water flow regime in the wetland

Dependent variable	Predictor variable	Unstandardized Coefficients		Standardized Coefficients Beta	t	Sig.	95.0% Confidence Interval for B	
		B	Std. Error				Lower Bound	Upper Bound
Carbon stock (Mg ha^{-1})	(Constant)	3.334	0.663		5.026	0.000	1.975	4.692
	Water discharge ($\text{m}^3 \text{ s}^{-1}$)	0.520	0.181	0.478	2.876	0.008	0.150	0.891

envisage that alteration of the micro-topography and flow in the tropical floodplain wetlands through anthropogenic activities such as quarrying, mining, impoundments, and landfills might affect the natural integrity of wetlands, leading to change in the plant species assemblages. Such changes in species assemblages might affect the carbon stocking potential of the wetlands, thereby affecting their role in providing valuable ecosystem services.

India has been a signatory to the Ramsar Convention on Wetlands as well as the Convention on Biological Diversity since the years 1986 and 1994, respectively (<https://www.ramsar.org>, <https://www.cbd.int>). However, efforts on conservation and judicious use of wetlands in the country still need to gain momentum, as only 115 wetlands have garnered attention under the wetland conservation programs like National Wetland Conservation Programme (<http://www.moef.nic.in>). Mainly, small-scale wetlands are under severe threat due to landfilling/reclamation and are primarily neglected (Bassi et al. 2014), though they perform essential ecological functions as evidenced through the present study. Therefore, we recommend that the national level programs must also focus on documentation, restoration, and conservation of small-scale seasonal wetlands that are providing valuable ecological services and playing a crucial role in regional climate change mitigation. In the present study, we have drawn the conclusions based on observations made in a single seasonal floodplain wetland, which may be a limitation from the perspective of representativeness of similar ecosystems in the tropics. Therefore, we strongly recommend that future studies should focus on diverse wetland types with contrasting morphometric and hydrological characteristics to understand the varied effect of hydrogeomorphic settings on the vegetation carbon stock and thus, the carbon stocking capacity of wetlands under different micro-climatic conditions.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s13717-019-0201-9>.

Additional file 1: Table S1. Distribution and density (no. of individuals ha^{-1}) of vegetation across various sampling stations of the wetland and Kruskal-Wallis test with habitat conditions under different sampling stations as the main effect variable; **Table S2.** One-way analyses of variance for micro-topography, water flow regime and vegetation attributes in the wetland with flood phases as the main effect variable; **Table S3.** Importance Value Index (IVI) of vegetation across various sampling stations of the wetland and Kruskal-Wallis test with habitat conditions under different sampling stations as the main effect variable; **Table S4.** Carbon stock (Mg ha^{-1}) of vegetation in different sampling stations of the wetland and Kruskal-Wallis test with habitat conditions under different sampling stations as the main effect variable; **Table S5.** Detailed results of multiple regression analysis (using backward method) for carbon stock in wetland vegetation against the micro-topographic parameters and water flow regime of the wetland; **Table S6.** Excluded variables in the multiple regression analysis (using backward method) for carbon stock in wetland

vegetation against the micro-topographic and water flow regime of the wetland.

Additional file 2: Figure S1. Flood-phase wise variations in species richness (a), Shannon-Wiener diversity index (b), Simpson dominance index (c), Buzas and Gibson's evenness index (d), and Taxonomic distinctness (e) of the wetland vegetation; **Figure S2.** Flood phase wise dominance-diversity curve of wetland vegetation in different sampling stations; a- Early flood phase, b- Mid-flood phase, c- Late flood phase; Station 1- inlet point 1; Station 2- middle point 1; Station 3- inlet point 2; Station 4- middle point 2 and Station 5- outlet point; **Figure S3.** Flood-phase wise variations in micro-topography and water flow regime of the wetland; depth (a), width (b), cross-sectional area (c), water velocity (d), and water discharge (e); **Figure S4.** Flood-phase wise variations in carbon stock in wetland vegetation

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Authors' contributions

All the authors contributed equally in the study design, data analysis, and preparation of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Available as supplementary information. The datasets supporting the conclusions of this article are included within the article and its additional files.

Ethics approval and consent to participate

Not applicable

Consent for publication

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Competing interests

The authors declare that they have no competing interests.

Author details

¹Department of Ecology and Environmental Science, Assam University, Silchar 788011, India. ²Department of Botany, North-Eastern Hill University, Shillong 793022, India.

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