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Impacts of river regulation and other anthropogenic activities on floodplain vegetation: A case study from Sri Lanka*

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Abstract: Since the initiation of large-scale development in late 1970s, the Mahaweli River basin in Sri Lanka has experienced significant changes. However, no comprehensive study has been undertaken so far to evaluate the impacts of river regulation on associated ecosystems including floodplains in the downstream. The present study was aimed at identifying the impacts due to both river regulation and other anthropogenic activities on inland floodplain habitats (locally known as *villus*) located along the final stretch of the River Mahaweli before reaching the Indian Ocean. Four *villus,* Handapana (HAN), Bendiya (BEN), Karapola (KAR) and Gengala (GEN), were selected for the study. HAN and BEN can be considered as highly influenced (HI) by river regulation while KAR and GEN as less influenced (LI) due to their respective locations. Due to the absence of pre- regulation vegetation data, HI *villus* were compared with LI *villus* in order to explore any potential impacts of river regulation. Vegetation was enumerated using belt transect method. To find out other on-going anthropogenic impacts on these *villu* ecosystems, a survey was conducted using 100 individuals living in two villages located nearby. The results revealed some significant modification in the composition and the diversity of the vegetation, most possibly due to river regulation and other on-going anthropogenic activities. However, the most notable changes were recorded in the herbaceous layer. Some native aquatic herbaceous species have been completely absent over the period of two decades since the developmental activities begun, while some exotic invasive aquatic species (*Eichhornia crassipes)* dominated the herbaceous layer in HI *villus* threatening the survival of the remaining native species. Density and richness of lianas too diminished significantly in HI *villus* perhaps due to changes of micro-habitat conditions as a result of river regulation and also due to over-harvesting for commercial purposes. The results suggest that these ecosystems have been altered over the years due to culmination of factors including altered flow regimes following river regulation and some on-going human influences. The present study highlights the importance of regulating such human influences on *villus* including fishing and extracting cane and reed in order to protect these vulnerable ecosystems for future generations. The potential of these ecosystems to develop ecotourism has also been emphasized.

Abbreviations: BEN–Bendiya; GEN–Gengala; HAN–Handapana; KAR–Karapola; MFNP– Mahaweli Floodplain National Park.

Nomenclature: Ashton et al. (1997), Vlas and Vlas (2008).

Introduction

Fluvial dynamics are vital in maintaining the biodiversity of riverine vegetation as well as lentic, lotic and semi-aquatic habitats (Ward et al. 1999). Construction of large headwater dams in river diversion projects alters inundation regimes in wetlands hence affecting their ecology (Dynesius and Nilsson 2994; Fraizer and Page 2006, Kingsford 2000). River regulation declines annual frequency of flooding in downstream habitats thereby altering the composition and regeneration of plants specific to these habitats (Kingsford 2000; Maingi and Marsh 2002, Layer 2005). Previous studies confirmed that the fauna and flora have been adversely affected due to reduced flood intensities in terminal wetlands following river regulation (Mac Nally et al. 2014, Bino et al. 1015, Catelotti et al. 2015). Layer (2002) also noted that the over-bank flooding is a critical factor in wetlands which determines species composition and distribution. While some plants in wetlands prefer highly fluctuating water tables others prefer somewhat stable conditions highlighting the importance of over-bank flooding in wetlands (Layer 1002). In addition to river regulation, other anthropogenic activities also influence these highly vulnerable habitats. Over exploitation of these habitats can occur through livelihoods of the local communities and construction of infrastructure facilities, which threaten these delicate habitats (Schindler 2001, Spackman and Hughes 1995). As a result, these floodplain habitats are slowly disappearing around the world.

* The Student Conference on Conservation Science (SCCS) is organized each year in several locations, Tihany at the Lake Balaton in Hungary being one of them. Since 2016, Community Ecology offers a prize at SCCS Tihany for the best presentation in the field of Community Ecology. An independent jury awards the prize that is an invitation to submit a manuscript to the journal. This is the paper of the first SCCS Tihany Awardee, Shalini Rajakaruna, back in 2016.

Inland freshwater wetlands associated with rivers are locally known as *villus* in Sri Lanka (IUCN-CEA, 2006). The *villus* are important ecosystems as they are the only naturally-formed stagnated freshwater bodies in the island (CEA, 1995). The *villus* are directly or indirectly connected to a main river through small waterways, thus their water retention is highly depend on their respective rivers. Mahaweli *villus* have been identified as highly threatened ecosystems mainly due to the major developmental activities carried out under the Accelerated Mahaweli Development Project (AMDP) in the late 1970s. River Mahaweli is the longest river in Sri Lanka, which starts from the central highlands and flows into the Indian Ocean from north-east of the island. Along the final stretch of the River Mahaweli (the stretch after the final tributary meets the river), there are 38 *villus* covering an area of 12,500 ha. The most noted characteristic of '*villus'* is that the main pool which is more or less persistently filled with water while its extended floodplain is inundated only during the rainy season (CEA, 1995). Prior to the implementation of this project, it was anticipated that the mean annual flow in the downstream will be reduced approximately by 50% after the completion of the project (CEA, 1995). These highly sensitive ecosystems are often surrounded by small hamlets, whose main livelihoods include paddy cultivation, cane harvesting, clay mining for brick making, vegetable and tobacco cultivation and inland fishery (IUCN-CEA, 2006).

However, after more than three decades since completion of AMDP, no study has been undertaken to assess the dam-induced impacts or other anthropogenic impacts on these highly vulnerable and ecologically important habitats, further highlighting the importance of the present study. Four *villus* located in the downstream of Mahaweli *viz.,* Handapana (HAN), Bendiya (BEN), Karapola (KAR) and Gengala (GEN) were selected for the study taking into consideration their specific locations in relation to the main river, Mahaweli. Due to the unavailability of data prior to the AMDP*,* the four *villus* was categorized as less and highly influenced (LI and HI) *villus*. Both GEN (hereafter GEN-LI) and KAR (hereafter KAR-LI) *villus* are located after the last major tributary meets the river, with the assumption that they are less influenced by river regulation, while HAN (hereafter HAN-HI) and BEN (hereafter BEN-HI) *villus* are located prior to the last tributary anticipating relatively more influences. We hypothesize that the vegetation density and richness is higher in LI than HI *villus* while species composition are significantly different between them.

Materials and methods

Description of study sites

The Mahaweli Floodplain National Park (MFNP) is situated in the North-Central Province of Sri Lanka, which comes under the Dry Zone. The area received most of its precipitation during the north-east monsoons (from September to February) with long intermittent dry spells with a mean annual rainfall of 1,750 mm (CEA, 1995). The mean monthly temperature is 28°C. The altitude varies between 0 – 50 m a.s.l. with an almost flat terrain including vast tracks of Dry Forests dominated by *Manilkara hexandra, Chloroxylon sweitenia* and *Terminalia arjuna*. HAN-HI and BEN-HI are twin *villus* located in the MFNP covering an area of approximately 796 ha. During the north-east monsoons, connective waterways feed HAN-HI and BEN-HI *villus* allowing them

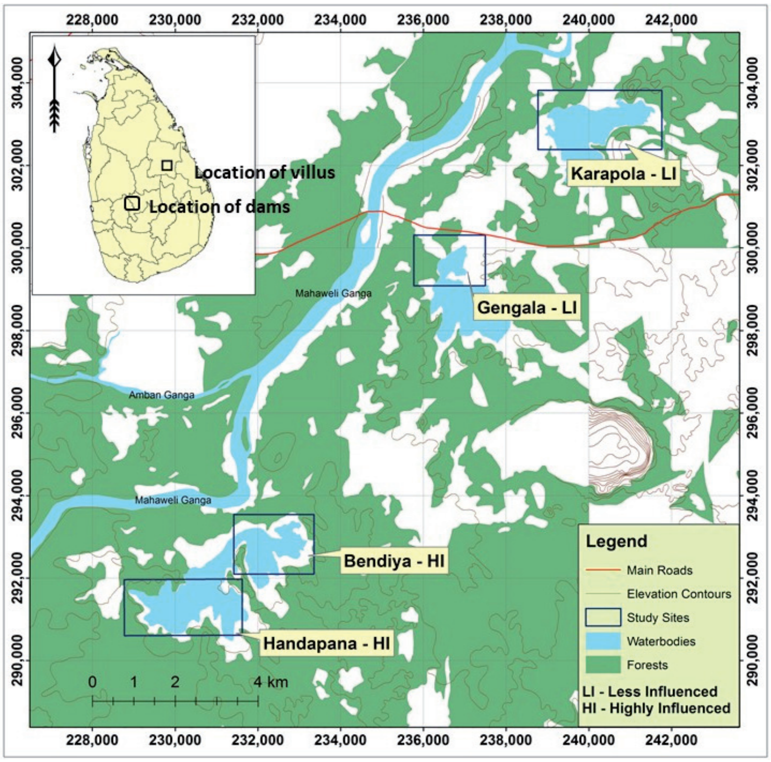

Figure 1. Locations of the highly-influenced (Handapana, Bendiya) and less-influenced (Karapola and Gengala) villus in Floodplain National Park in the North Central Province of Sri Lanka.

to retain water more or less throughout the year. KAR-LI, also a perennial *villu,* covers anarea of 552 ha. GEN-LI *villu* is comparatively smaller in size (264 ha) and dries out periodically (CEA, 1995). HAN-HI and BEN-HI *villus* are located prior to the last major tributary meets the river Mahaweli. After the last tributary empties its water into the Mahaweli, the river flow becomes more or less natural until it flows to the Indian Ocean at the Koddiyar Bay in the north-east of the island. KAR-LI and GEN-LI *villus* are located after the major tributary meets the Mahaweli and are situated approximately 4 km apart (Fig. 1).

Quantification of the floodplain vegetation

In each study site, three belt transects were randomly established to three different directions from the main pool towards the upland vegetation. All transects started from the shallow waters were extended across the marginal floodplain towards the upland vegetation. Each transect (100 m × 10 m) was divided into ten, 10 m × 10 m quadrats, totaling 30 quadrats in each study site. The vegetation was enumerated under different categories (trees, shrubs, lianas, herbs and graminoids). The trees were divided into two age groups; mature individuals (individuals ≥ 5 cm dbh) and saplings (individuals < 5 cm dbh). The mature individuals were further categorized into 5 girth classes. Both aquatic and terrestrial herbaceous species were categorized under 'herbs'. Grasses and sedges were categorized as 'graminoids'. The percentage cover values were visually estimated for herbs and graminoids. All individuals of graminoids were identified to their generic level while trees, shrubs, lianas and herbs were identified to their lowest possible taxonomic ranks. Schematic vegetation profile diagrams of *villus* were constructed using the software Inkscape version 0.91 at a scale of 1 cm: 2 m.

Socio-economic survey

The survey was conducted (through face-to-face interviews) using a random sample of 100 individuals representing 100 households in two small hamlets (Karapola and Sewanapitiya) located in close proximity to study sites. The information was collected using a questionnaire to gather the socio-economic status of villagers, their interactions with *villus* and their attitudes towards conservation of *villu* ecosystems. The questionnaire is given in supplementary document 2. The attitudinal scales were composed of equal numbers of favorable and unfavorable statements. For the questions on conservation attitudes, interviewees were asked to respond to each statement in terms of their degree of agreement (agree, disagree or neutral) or position (positive, negative or neutral) (Pyrovetsi and Daoutopoulos 1989).

Data analysis

The Shannon and Pielou diversity indices were calculated to compare vegetation diversity (herbs and graminoids were excluded in the calculation). To test the significance of densities, cover values and species richness of different vegetation categories (trees, shrubs, lianas, herbs and graminoids) between study sites, a one-way Analysis of Variance (ANOVA) was performed. The data was checked for normal distribution using Shapiro-Wilk normality test prior to the analysis. Since the data was not normally distributed, data was transformed into square root values prior to the analysis. Pairwise mean comparisons were done using Tukey's test. Data analysis was done using the statistical package Rcmdr: R Commander. R package version 2.4-1 (Fox 2017) and the graphs were constructed in Microsoft Excel 2010.

Regression analysis was done using IBM statistics 20 to observe correlations between study variables (variables given in Table 2). For the survey, scale scores for level of agreement for the answers given for questions on conservation opinions were computed by summing the response scores of the component items with the given responses, using the following integer values for favorable statements: 1, strongly disagree 2, disagree 3, neutral 4, agree and 5, strongly agree. The weighting scheme was reversed for unfavorable statements, so that higher scores always indicate more favorable attitudes towards conservation.

Results

Vegetation structure

All *villus* had distinct horizontal zonation of vegetation, except at KAR-LI (Figs 2 and 3). The pools were mainly dominated with aquatic herbs and grasses while the pool margins and the immediate floodplains were dominated with hygrophilous plants. Dry zone species were recorded away from the main pool towards the upland vegetation. In contrast to other *villus*, KAR-LI showed no clear horizontal zonation (Fig. 3a). The upland vegetation was denser at HAN-HI with the canopy layer reaching about 20 m in height (Fig. 2a) and at BEN-HI, the canopy trees were more scattered with a maximum height of 30 m. The KAR-LI and GEN-LI *villus* had discontinuous canopy layers reaching up to a stature between 18 – 20 m. HAN-HI and BEN-HI *villus* had comparatively larger pools than that of KAR-LI and GEN-LI. The vertical zonation was clear in all *villus* with three distinct vegetation layers, canopy, sub-canopy and ground vegetation

Floristic composition and diversity

A total of 134 plant morphospecies were recorded in all four *villus,* belonged to 58 herb, 39 graminoids, 27 trees, 7 shrubs and 3 liana species, out of which 100 morphospecies (including five most abundant graminoids) were identified to their species levels, belonging to 20 families. Out of 100 identified species, only 7 species were recorded in all four *villus*. They included 3 trees (*Vitex leucoxylon, Barringtonia racemosa, Bauhinia racemosa)*, a shrub *(Flueggea leucopyrus*), a liana (*Calamus rotang*), a herb (*Alternanthera sessilis*) and a graminoid (*Cyperus rotundus*). Furthermore, 13, 24, 7 and 8 species were recorded exclusively in HAN-HI, BEN-HI, KAR-LI and GEN-LI *villus,* respectively. From

Table 1. Total number of, families, species and individuals, and Shannon Diversity and Pielou's evenness indices (only trees and shrubs and lianas were used for the calculation) in HI and LI villus in Mahaweli floodplains in Sri Lanka.

	Number of Families	Number of Species	Number of individuals (Trees + shrubs + lianas)	*Shannon Diversity index	*Evenness-Pielou's Index
Highly influenced villus (HI)					
HAN-HI	29	36	470	0.96	0.31
BEN-HI	36	61	268	2.11	0.75
Less influenced villus (HI)					
KAR-LI	31	43	615	1.61	0.51
GEN- LI	24	29	495	2.99	1.10

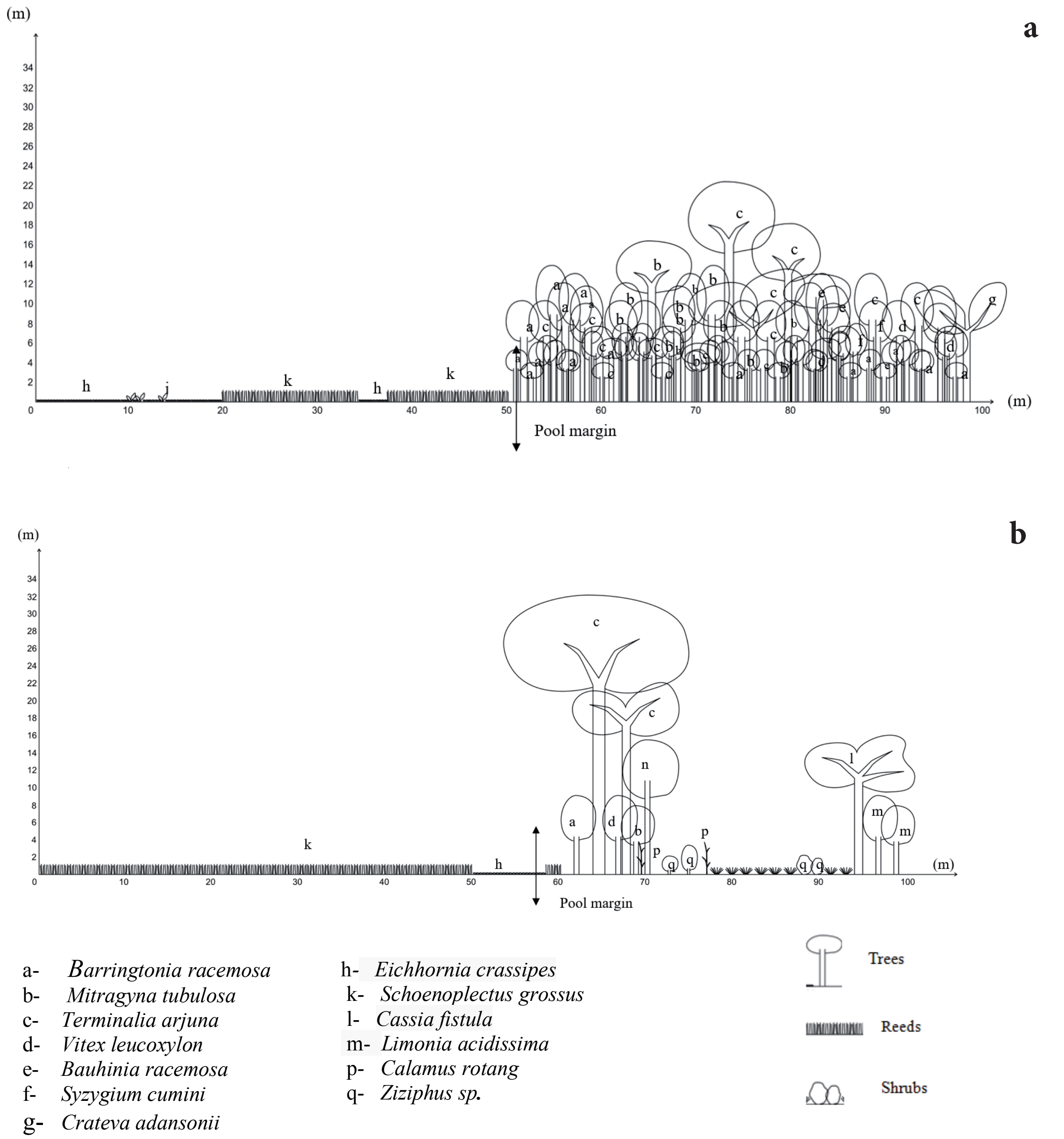

Figure 2. Schematic vegetation profiles of highly influenced villus. **a)** HAN-HI; **b)** BEN- HI along a 100 m transect running from the main pool towards upland vegetation. Pool margin is indicated by a two headed arrow. Different letters indicate different species.

these exclusive species, the majority (43 – 87%) belonged to the herbaceous layer. Complete species list is given in the Supplementary Material, Table 1.

The highest diversity and evenness indices were recorded at GEN-LI (2.99 and 1.10, respectively) while the least at HAN- HI (0.96 and 0.31, respectively). Interestingly, all four *villus* were dominated with native tree and shrub species (between 98 - 100%). The most abundant native tree species was *Barringtonia racemosa* (L.) Spreng (with relative abundances ranging from 34 – 81%). *Terminalia arjuna* (Roxb.) Wight & Arn. (8 – 30%) and *Bauhinia racemosa Lam.* (3 - 12%) were also recorded in relatively higher numbers compared to others. The proportion of exotic tree species was extremely low in all study *villus* (> 2 % in every study site). *Cassia fistula* was the most abundant exotic tree species. A native shrub, *Calotropis gigantea,* dominated at HAN-HI and KAR-LI (≈ 55 and 46 %, respectively) while *Fluggea leucopyrus* dominated in BEN-HI and GEN-LI *villus* (≈ 72 and 67 %, respectively). *Calamus rotang* was the most abundant liana species in KAR-LI and GEN-LI and BEN-HI *villus*. *Ziziphus oenoplia* (a liana) was only recorded at HAN-HI. In BEN-HI, the exotics dominated the herb layer in comparison to other *villus* (≈ 63%), and this was mainly due to the extensive growth of the aquatic herb, *Eichhornia crassipes*, a known invader in Dry Zone reservoirs. In both HI *villus*, *Eichhornia crassipes* showed higher relative abundances (28% and

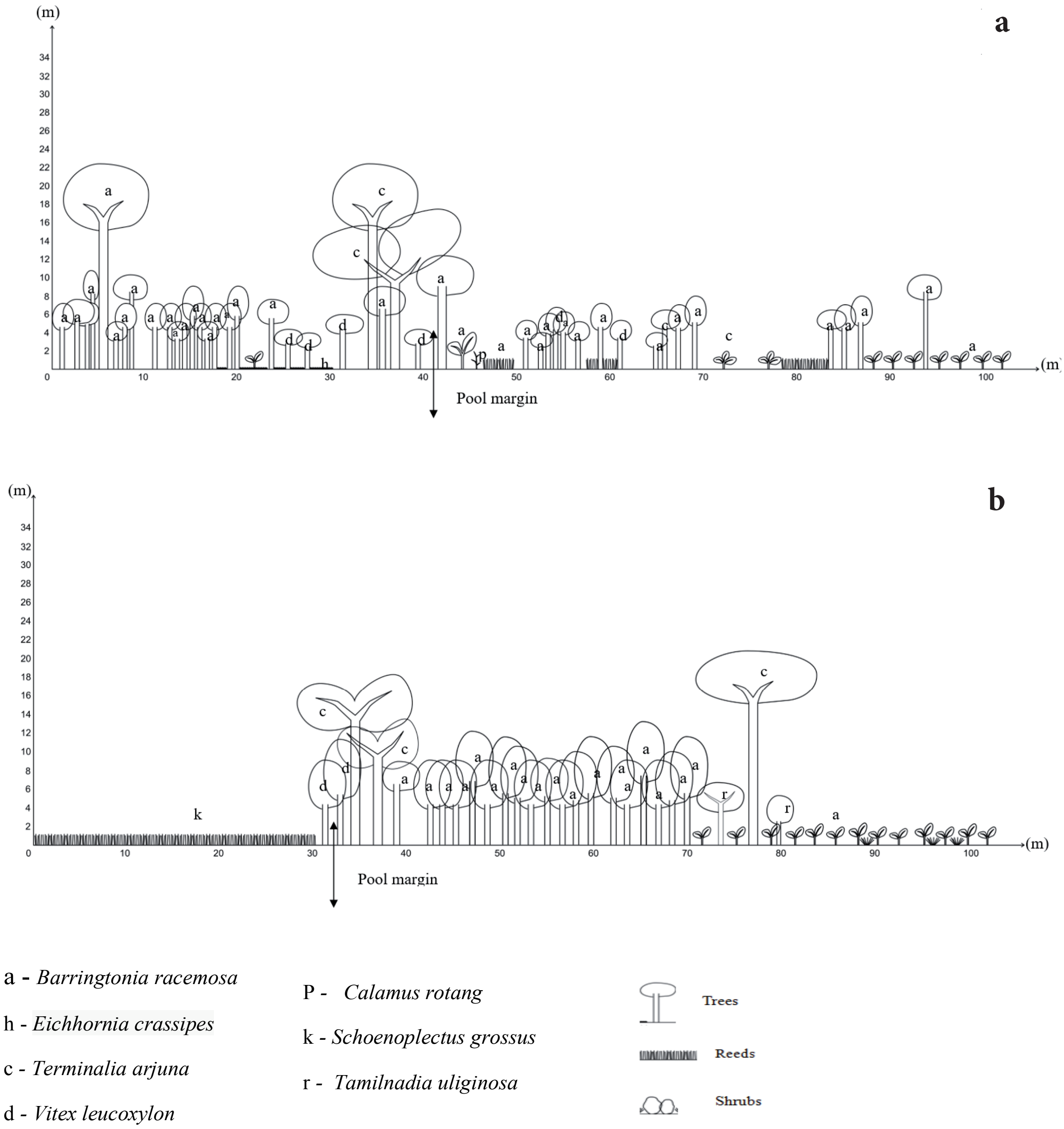

Figure 3. Schematic vegetation profiles of less influenced villus. **a)** KAR-LI; **b)** GEN-LI along a 100 m transect running from the main pool towards upland vegetation. Pool margin is indicated by a two headed arrow. Different letters indicate different species.

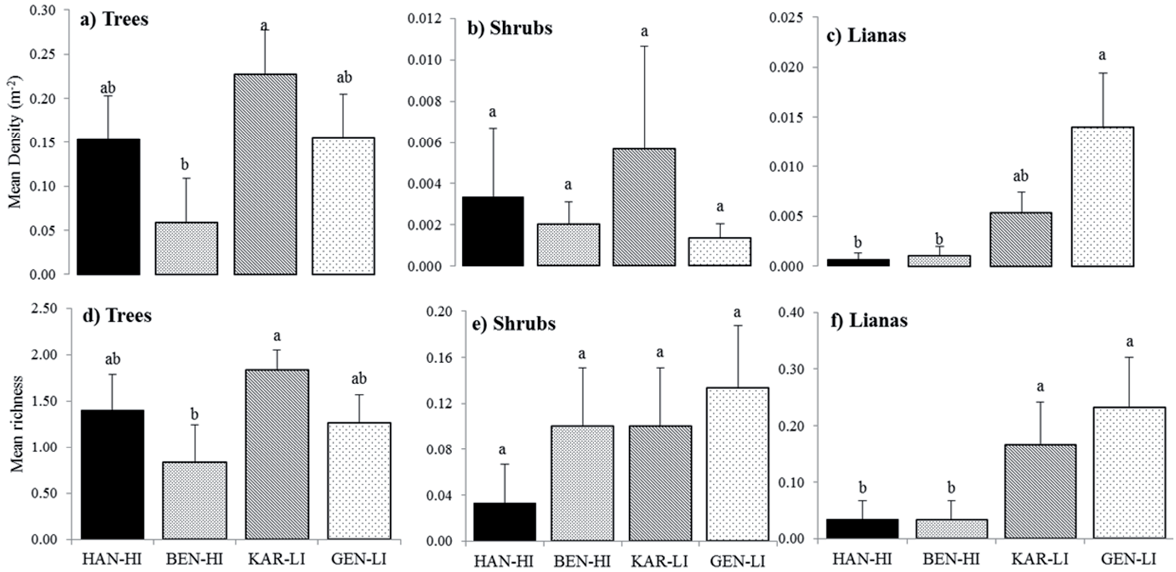

Figure 4. Mean density of **a)** trees (m-2), **b)** shrubs, **c)** lianas (ANOVA; F= 3.544 p = 0.024, F= 2.553 p = 0.070 and F = 4.992 p = 0.005, respectively). Mean richness of **d)** trees (m-2), **e)** shrubs, **f)** lianas (ANOVA; F= 2.461, p = 0.0241 and F = 0.76, p = 0.524 and F = 6.411, p = 0.0013, respectively) in the four study villus (HAN-HI, BEN-HI, KAR-LI and GEN- LI). Different letters indicate significant differences between villus. Vertical bars represent the standard errors of mean (SEM) value.

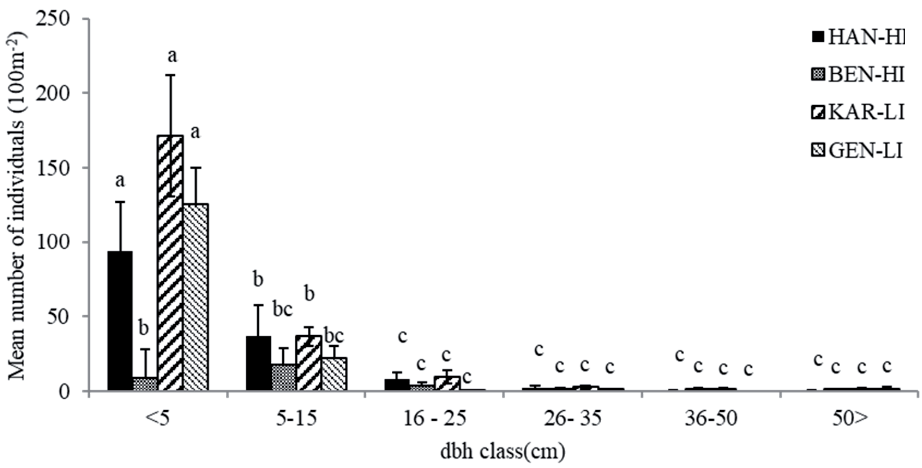

Figure 5. The girth class distribution of trees (per 100 m2) in study sites; HAN-HI, BEN-HI, KAR-LI and GEN-LI. Vertical bars represent the standard error of mean (SEM). Significant differences are highlighted using different lowercase letters.

26%, respectively) compared to LI *villus* (2.9 and 0%, respectively). Graminoids belonging to the families Poaceae, Juncaceae, Typhacea and Cyperaceae were recorded in all four *villus*. The most abundant species was *Schoenoplectus grossus* (Cyperaceae), which prefers moisture-rich soils near stagnated water bodies.

Density and species richness

KAR-LI has recorded significantly higher tree density and richness than that of BEN-HI, with no differences with HAN-HI and GEN-LI *villus* (Figure 4). However**, t**he density and richness of shrubs showed no significant differences between study *villus*. Lianas, on the other hand demonstrated significantly higher density and richness in both LI *villus* compared to that of HI *villus*. In the study, tree seedlings were rather rare in all *villus*. The density of saplings was higher in LI *villus* than that of HI *villus*. The girth class distribution curves were 'Inverted J' shaped in all study *villus*, except at BEN-HI (Fig. 5).

The herb cover (which includes both aquatic and terrestrial herbs) was higher at HI *villus* compared to that of LI *villus* (Fig. 6a). An excessive growth of *Eichhornia crassipes* along pool margins was a common sight at HI *villus*, contributing to this significant difference between HI and LI *villus*. The study also revealed a significantly higher graminoid cover at GEN-LI compared to that at HAN-HI (Fig. 6b).

Table 2. Regression Analysis (using IBM SPSS Statistics 22) between villagers' total monthly income and some of their livelihood characteristics. The probability values indicating significant differences are highlighted.

	Unstandardized Coefficients of variation[a]		Standardized Coefficients of variation[a]	t value	Level of significance
		St. Error			
(Constant)	9.307	0.312		29.871	0.000
No. of dependents	0.120	0.050	0.255	2.416	0.018
Education	0.072	0.019	0.387	3.770	0.000
Land area	-0.564	0.280	-0.210	-2.017	0.047
Agriculture	0.097	0.163	0.061	0.593	0.555
Fisheries	0.034	0.154	0.023	0.218	0.828
Extracting Cane	0.024	0.197	0.013	0.119	0.905
Reed Harvesting	0.230	0.251	0.093	0.916	0.363
Firewood	-0.321	0.161	-0.201	-1.999	0.049
Cattle feed	-0.063	0.395	-0.016	-0.159	0.874
Recreation	-0.186	0.181	-0.109	-1.028	0.308

a) Dependent Variable: lnTMIncome (Total monthly income in log form).

Table 3. The mean scale scores by taking averages of the response scores using the following integer values for favorable statements: 1, strongly disagree 2, disagree 3, neutral 4, agree and 5, strongly agree. The weighting scheme was reversed for unfavorable statements; higher scores always indicate more favorable attitudes towards conservation.

Villagers' attitudes towards villus	Mean score	Results
We depend on the ecosystem (ES) services that villus provide	3.79	Agree
Our future will be benefitted from ES services of villus	4.58	Strongly agree
We should conserve villus for the benefit and existence of flora and fauna	4.25	Agree
I have little or no interest in the villus environment	2.59	Disagree
I think that the local community has a responsibility for the protection of the villus environment	4.22	Agree
Eco-tourism should be developed in villus for sustainable income	3.63	Agree
The Government should do more to protect the villus environment	3.97	Agree
Villus should be preserved for the benefit of my children and future generations	4.15	Agree
Reforestation is important to preserve villus environment	4.35	Agree
Conservation of wetlands is important for the sustainability of villus	4.39	Agree
Development activities that destroy villus should be banned	3.14	Neutral

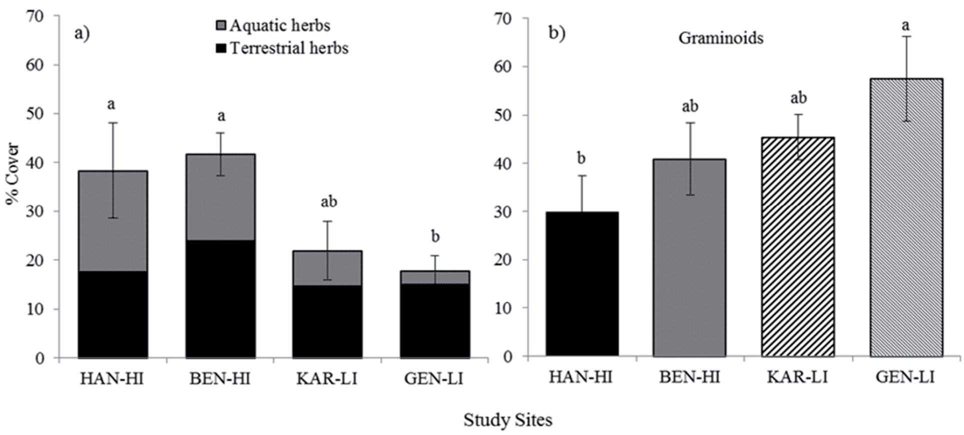

Figure 6. a) Mean vegetation cover of herbs (as a percentage per m^2) (ANOVA; F= 4.88, p = 0.006) and **b)** mean vegetation cover of graminoids (as a percentage per m^2) in the four villus; HAN-HI, BEN-HI, KAR-LI and GEN- LI (ANOVA: F= 2.84, p = 0.051). Different letters indicate significant differences between villus. Vertical bars represent the standard errors of mean (SEM) values (calculated for total herb cover).

Socio- economic status of villagers

The interviewees were in an average age of 40 years and the ratio of male to female was 2.8:1. The study population was belonged to three ethnic groups *viz.,* 52 % Sinhalese (the major ethnic group in the island), 40 % Tamils and 7% Muslims, representing a multi-cultural community. The average education level of the study population was rather low (up to the sixth grade according to the Sri Lankan education system), with 12% of them had no formal education what so ever. The main source of income was through agriculture (40 %) followed by other non-skilled occupations in the government and private sectors (34 %). Some were relied on inland fisheries (26 %) while others by selling cane and reed (11%), where both activities centered around *villus*. The average monthly income was 19,433.00 Sri Lankan rupees (LKR) with a total monthly income ranged between 2,000 to 60,000.

Association with villu vegetation and other services and products

The villagers living close by depend on various products and services offered by *villus*. The villagers use *villus* mainly for their recreational activities (20.5%), and to gather non-timber forest products such as medicinal plants (18%), firewood (18%) cane and reed (6%) etc. Apart from the uses of vegetation, the villagers used *villus* for fishing (12%) and to provide irrigation facilities for their crops (8.5%). Only 18% of villagers totally depend on *villus* for their monthly income while 21 % with zero financial benefits from *villus*. Moreover, 46 % of villagers acquired 50 % of their monthly income from products and services offered by *villus*, indicating their high dependence on these ecosystems.

Regression analysis revealed a positive correlation between the villagers' dependence on *villus* with their monthly income (Table 2). The level of education and number of dependents in a family were also significantly correlated with the monthly income of the families. Though, the land ownership generally may contribute positively towards the monthly income in a household, in the present study it showed a negative impact, indicating higher the land ownership lesser the income.

Attitudes of villagers towards villus

The villagers have identified some anthropogenic activities that may cause negative impacts on *villu* vegetation. Burning large trees by trespassers has been identified as a major threat (21%) to these ecosystems, followed by river regulation (17%), illegal agriculture (16%), over harvesting of reeds and canes (13%) and over grazing by cattle (6%). Illegal fishing and poaching were identified as major threats to the fauna in *villus*. The villagers strongly agreed that their future will be more secure if these ecosystems are well conserved (Table 3). At the same time, the villagers also acknowledge the importance of developmental activities that may affect *villus* negatively. They agreed that eco-tourism should be developed in villus for a sustainable income for the villagers (Table 3).The survey also revealed the enthusiasm of villagers to take part in community-based activities (i.e., tree planting) conducted by the Forest Department of Sri Lanka to conserve and restore *villus*.

Discussion

Out of the four *villus*, higher diversity and evenness (in terms of trees, shrubs and lianas) was recorded at GEN-LI. GEN-LI was smaller in size compared to the rest of the study *villus* and dries out periodically. It refills naturally as the water level in Mahaweli River rises up. Therefore, GEN-LI experienced more or less natural inundation regime compared to other study *villus*. The 'Intermediate Disturbance Hypothesis' predicts that moderately disturbed sites support more diverse communities than that of too rare or too frequently disturbed sites (Roxburgh et al. 2004). In support, the lowest diversity and evenness indices were recorded at HAN-HI which is constantly disturbed by regulated water flows.

Irrespective of the level of influence due to river regulation, both tree and shrub layers were dominated by native tree species, with extremely low prevalence of exotics. Marks et al. (2014) have also observed a clear reduction of woody invasive species in floodplain forest assemblages that experience disturbances such as frequent flooding, perhaps supporting the fact that floodplains are generally resistant to woody invasive species. Zefferman et al. (2015) noted that plant communities that are abiotically stressful (or categorized as harsh) are reported to be less invaded by non-native species due to propagule limitation and invasion resistance. Interestingly, both LI *villus* had higher density and richness of lianas compared to HAN-HI and BEN-HI, indicating negative impacts of human-induced hydrological and habitat alterations caused by river regulation. In contrast, lianas are known to respond positively to disturbances in terrestrial habitats by increasing their vegetative (clonal) reproduction (Ledo and Schnitzer 2014). However, the present results suggest otherwise indicating that the liana response to disturbances may differ depend on their habitat characteristics. A woody liana, *Calamus rotang* is one of the most economically important plant species growing in *villus*. The villagers rightly identified the excessive extraction of *C. rotang* from *villus* may cause detrimental impacts on its communities. The flexible stem of this liana is used to make high-quality cane products. Therefore, excessive harvesting of this plant from the wild for commercial purposes can be identified as a major threat to its natural populations. *C. rotang* was recorded as absent in both HAN-HI and BEN-HI *villus* (both presumed as highly influenced) in a prior survey conducted by the Central Environmental Authority in 1995. However, during the present study *C. rotang* was recorded at BEN-HI *villu*.

The over-bank flooding (frequency and duration) in wetlands is a decisive factor in maintaining the species composition and distribution of floodplain vegetation as they generally prefer highly fluctuating water tables in comparison to terrestrial plants (Layer 2002, Murray-Hudson 2009). However, human-induced disturbances including river regulation can alter the frequency and duration of flood events in *villus*. In the present study, HI *villus* recorded consistently higher presence of exclusive species (13–24%) compared to LI *villus* (7–8%) with only 7 species shared by all study sites. The results suggest compositional differences between HI and LI *villus* most possibly due to habitat alterations as result of human disturbances. Reduced flood events due to river regulation make floodplain vegetation follow rather dry land succession in between flood pulses in seasonal *villus*. In the present study, all *villus*, except GEN-LI, showed perennial nature in spite of river regulation. However, no consistent differences were observed in the vegetation between perennial and seasonal *villus* in the present study.

The saplings of (mainly of *Barringtonia racemosa* and *Terminalia arjuna* which were the common canopy species in these *villus*), were observed in higher densities at LI *villus* than in HI *villus*, indicating higher regeneration potential in *villus* less-influenced by human activities. Presence of saplings of common overstorey species indicates a better regeneration potential of the particular vegetation (Lehvavirta et al. 2002). The girth class distribution curves also produced 'inverted J-shaped curves in all *villus*, except at BEN-HI, indicating stable equilibrium of plant communities, where mortality rates are being compensated by the regeneration rates (Pascal 1988). In all study *villus,* individuals belonged to the dbh class of 5 – 35 cm were more abundant than that of mature trees.

Shrubs are one of the most prominent life forms in dry-mixed evergreen forests in Sri Lanka, which is the most dominant vegetation type in the study area. However, in the present study, shrubs were observed in rather low densities in *villus* with the existing shrubs were scattered in the landscape while herbs and graminoids dominate the ground vegetation. In *villus,* herbs and graminiods are more abundant as they have the potential to establish in gaps created by disturbances (Pausas and Austin 2001). Herbaceous species generally have short life cycles while graminoids are annuals, and therefore they can spread and establish well in floodplain habitats where both natural and human-induced disturbances are more prevalent.

Eichhornia crassipes was the most dominant aquatic herb in both HI *villus*. *Eichhornia* is an invasive species that prevail in inland freshwater bodies with high nutrient contents and therefore considered as an indicative plant for low water quality (Villamagna and Murphy 2010). A survey carried out previously has recorded a total of 26 aquatic herb and graminoid species at HAN-HI and BEN-HI *villus* (CEA, 1995) and another study recorded 22 species (Tolisano *et al.* 1993). However, the current study has recorded a total of only 10 aquatic herb and graminoid species from the same *villus*, indicating a possible decline of species richness over a span of two decades. This speedy decline of aquatic species in HAN-HI and BEN-HI *villus* is probably due to the adverse impacts caused by the spread of *E. crassipes*. The studies indicate that high multiplicative ability of *E. crassipes* can impose high competition on the native flora, hindering their growth and survival (Jafari 2010). Previous studies too have noted that high coverage of E. *crassipes* can reduce sunlight penetration and oxygen content in water, thereby negatively affecting the native, submerged species (Villamagna and Murphy 2010). According to the survey carried out by CEA (1995), the most abundant aquatic herbs observed along the pool margin were *Aponogeton crispus*, *Nelumbo nucifera* and *Nymphaea stellata,* which are all native to Sri Lanka. In the present study, none of these species were recorded in the study, suggesting the most detrimental influence on the herbaceous cover than on trees and shrubs. However, due to differences in sampling methods in the survey by CEA (1995) and the present study conducted by us, results cannot be statistically compared. However, the disappearance of number of aquatic species from study *villus* may have possibly caused by the extensive spread of *E. crassipes* or else due to the alterations of micro-habitat conditions due to changing flow regimes in these water bodies. However, no previous vegetation records were available from LI *villus* for a similar comparison. In the current study, only eight aquatic herbaceous species were recorded in LI *villus*, which was lower than the number of species recorded in HI *villus*.

The most dominant graminoid species in all study *villus* was *Schoenoplectus grossus*. This is another economically important species growing in these distinct ecosystems. The leaves of *S. grossus* are used to weave reed mats and baskets and it is a common home-based occupation among women living in the area. The graminoid cover was significantly higher at GEN-LI than the rest of *villus*. GEN-LI is a seasonal *villu* where the vegetation succession was more conspicuous as it undergoes prolonged dry periods and experiences natural floods during the rainy season. In wetlands, grasses and sedges are present in high densities during succession before reaching the equilibrium (Odland and del Moral 2002). The seasonal fluctuations may be one of the reasons for higher graminoid cover in GEN-LI compared to other study *villus*. Furthermore, the presence of economically important plant species in *villus* may also increase the chances of anthropogenic activities in these ecosystems.

The results of the present study suggest that river regulation together with other human activities has changed the composition of *villus* in Mahaweli Floodplains. The villagers living nearby rely on *villus* for their day-to-day activities. Although *villus* are popular among the locals as a recreational site, they are not generally popular among other local and/or international tourists. Therefore, it is high time for policy makers to take initiatives to popularize these distinct habitats as sites of tourist attractions. The *villus* provide best sites to watch wild life, especially large herds of elephants and flocks of local and migratory birds, and therefore has a huge potential to develop them as sites of tourist attraction. However, it is vital to take necessary measures to protect these ecosystems, as too many visitors may bring about more threats to these vulnerable ecosystems. The villagers acknowledged the importance of developing eco-tourism in *villus* as this may eventually increase their economic status as well. A community-based approach to ecotourism is being recognized as a tool to promote both the quality of the people lives and also the conservation of resources (Scheyvens 1999). The opportunity to enhance development potentials by exploiting natural resources without destroying them cannot be denied, hence sound understanding of basic factors critical in planning and managing such sustainable developmental activities (Cater 1993). In addition to recreational activities, a significant number of villagers depend on *villus* for their day to day income. Their high dependence on these ecosystems can also lead to detrimental impacts on the biodiversity of these highly vulnerable ecosystems, unless measures taken by the authorities to regulate their activities. According to the villagers, illegal fishing in *villus* was one of the major threats to these ecosystems as they use illegal fishing practices including the use of poisons and dynamite in fishing. The results also suggest that that the villagers are aware of the common threats to the biodiversity in *villus* and therefore they strongly agreed with the fact that *villu* ecosystems should be conserved at all cost. However, the villagers emphasized the importance of carrying out developmental activities in the area without destroying the *villu* ecosystems. They also agreed that reforestation is one important measure to restore these degraded ecosystems.

Finally, the present study suggests that the river regulation together with other human-induced activities can cause significant changes in the composition and richness of these distinctive ecosystems. The study also highlights the importance of products and services provided by *villus* to the people living nearby, stressing the importance of taking immediate measures to regulate some of these activities in order to minimize their detrimental impacts on *villus*. The community-based conservation measures can be the best option taking into consideration the villagers' enthusiasm and understanding towards conservation of *villus*.

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Supplemetary material

Appendix S1. List of species recorded during the study.

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