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Mangrove community recovery potential after catastrophic disturbances in Bangladesh

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ABSTRACT

The objective of this study was to compare the variation in the soil seed banks and the aboveground vegetation in relation to three habitats, i.e., swamp forests, grassland and sand dunes within the Sundarbans mangrove forests of Bangladesh. We collected vegetation data (species and their percentage cover) by using quadrat sampling: 10 m $\times$ 10 m for swamp forests and 5 m $\times$ 5 m for grassland and sand dunes. We estimated the density of viable seeds of species in the seed bank by counting germinants from soil cores in a germination chamber. Species richness and composition of both aboveground vegetation and the soil seed banks differed significantly among habitats. We identified a total of 23 species from the soil seed bank. Of these, two were true mangrove species and the remaining were non-mangrove species, including halophytic grasses, herbs and mangrove associate species. Our results confirm that mangrove species do not possess a persistent soil seed bank. The presence of high-density non-mangrove and associated mangrove species in the soil seed bank implies that after frequent catastrophic disturbances which limit incoming propagules from adjacent forest stand, large canopy gaps can easily become invaded by non-mangrove and mangrove associate species. This would result in the formation of a cover of non-mangrove species and cryptic ecological degradation in mangrove habitats. We suggest that forest managers should actively consider gap plantations with mangrove species in the large canopy gaps created after catastrophic disturbances to counteract the invasion of non-mangrove species and cryptic ecological degradation.

1. Introduction

Understanding soil seed bank dynamics is critical for predicting the survival and continued existence of a species in a particular habitat (Greene and Waters, 2001; Harper, 1977; Kellerman, 2004). Often, the soil seed bank is recognized as insurance against plant extinction in the event of drastic habitat disturbances (Rees, 1996; Thompson, 1992). Mangrove species do not persist for long periods in soil seed banks (Fransworth, 2000; Ungar, 2001), but many salt tolerant non-mangrove and mangrove associate species can persist in seed banks under mangrove forests. Since most mangrove species have viviparous and crypto-viviparous germination and recalcitrant seeds (Fransworth, 2000), the importance of seed bank species is rarely emphasized in vegetation development and succession in mangroves. However, mangrove seed bank species could play an important role in vegetation development, especially if we assume catastrophic disturbances that cause severe damage to the adjacent mangrove vegetation and ultimately limit the supply of propagules.

Located at the land–sea interface, mangrove vegetation usually experiences periodic cyclonic storms, tidal surges and floods. The conventional wisdom is that mangrove vegetation often recovers quickly after these disturbances. Typically, incoming propagules from adjacent forest stands and advanced regeneration that survived the disturbance, facilitates this recovery process (Roth, 1992; Sherman et al., 2001). However, when disturbance events are unusual, then the type and patterns of recovery remain uncertain. In recent years, the frequency and intensity of catastrophic disturbances in tropical coastal areas have increased due to climate change (Houghton et al., 2001; Solomon et al., 2007). For instance, within a short period, the Sundarbans mangrove forests have encountered

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five major unusual catastrophic events, i.e., cyclones in 1988 and 1991, the Asian tsunami in 2004, cyclone Sidar in 2007 and cyclone Nardis in 2008. These disturbances have caused enormous amounts of damage to the standing vegetation of the Sundarbans mangrove forests. In some areas of the Sundarbans, i.e., the offshore islands, these catastrophic disturbances have resulted in the complete destruction of mangrove vegetation. This damage leads towards uncertainty in the availability of incoming propagules, essential in typical mangrove vegetation recovery. Thus, after the 2004 Asian tsunami, as well as after cyclone Sidar and cyclone Nardis, the following open questions were posed: will the degraded mangrove forest ever recover? If so, what could be the composition of the vegetation?

Species composition of the soil seed bank can help predict the vegetation recovery pattern in these type of situations. Soil seed banks are very important because once seeds are buried in the soil, these seed may escape the disturbance (Chang et al., 2001). Since most mangrove species do not possess a persistent soil seed bank (Fransworth, 2000), the significance of soil seed banks is rarely emphasized in mangroves. However, it is important to know the presence of non-mangrove and mangrove associate species in the soil seed bank since, in the absence of propagules of mangrove species, these non-mangrove species could quickly occupy the vacant mangrove habitat.

The extent of the damage of mangrove vegetation after a catastrophic disturbance can be estimated from aerial photographs (Giri et al., 2007) but the nature and extent of soil seed banks needs empirical evaluation. Studies of the species composition in the soil seed bank and its comparison with aboveground vegetation although limited, is not uncommon in saline wetlands (Chang et al., 2001; Delgado et al., 2001; Egan and Ungar, 2000; Hartman, 1988; Hopkins and Parker, 1984; Matlack and Good, 1990; Ungar, 2001; Ungar and Woodell, 1993). However, most of these studies were from forests that are characterized by very few true mangrove species. There is still little information available on the seed banks of tropical mangrove forests that are floristically rich and characterized by many true mangrove species.

In our study, we evaluated the species composition of soil seed banks in the Sundarbans mangrove forests of Bangladesh, biologically some of the most diverse mangrove forests in the world. We further tested if the characteristics of the soil seed banks (size and composition) varied among the three habitats within the mangrove forests: swamp forests, grasslands and sand dunes. Specifically, we asked three questions:

(i) Does the soil seed bank species richness and composition differ among the three habitats in the Sundarbans mangrove forest?
(ii) Does the aboveground vegetation (richness and composition) differ among the three habitats in the Sundarbans mangrove forest?
(iii) Do soil seed bank species correspond to aboveground vegetation in the Sundarbans mangrove forest?

Based on answers to these questions, we discuss the paths of vegetation recovery and the risks of biological invasion after catastrophic disturbances.

2. Methods

2.1. Site description

The study was conducted in the Katka-Kochikhali area within the Sundarbans mangrove forests of Bangladesh (between latitude 21°31′ and 22°30N′ and longitude 89° and 90°E; Fig. 1). The Sundarbans represents the largest single tract of mangrove forest in the world, situated along the coast of the Bay of Bengal with a geographical spread over Bangladesh (~60% of total area) and India (~40% of total area) (Das and Siddiqi, 1985). Biologically, this forest is the most diverse mangrove ecosystem that supports no less than 334 plant species, including 62 true mangrove species. This forest receives perennial freshwater flows from upstream rivers and is also affected by tide and saline water from the Bay of Bengal. These forests regenerate naturally (Iftekhar and Islam, 2004; IUCN-Bangladesh, 2003).

Salinity and tidal surges are the major determinants of the Sundarbans mangrove vegetation (Ellison et al., 2000). Ecologically, the Sundarbans have been divided into three zones, based on salinity: (i) freshwater, (ii) brackish water and (iii) a saline zone (Das and Siddiqi, 1985). Our study area (Katka-Kochikhali) falls within the southeastern part of the Sundarbans. Although the eastern part of the Sundarbans is typically known as a freshwater

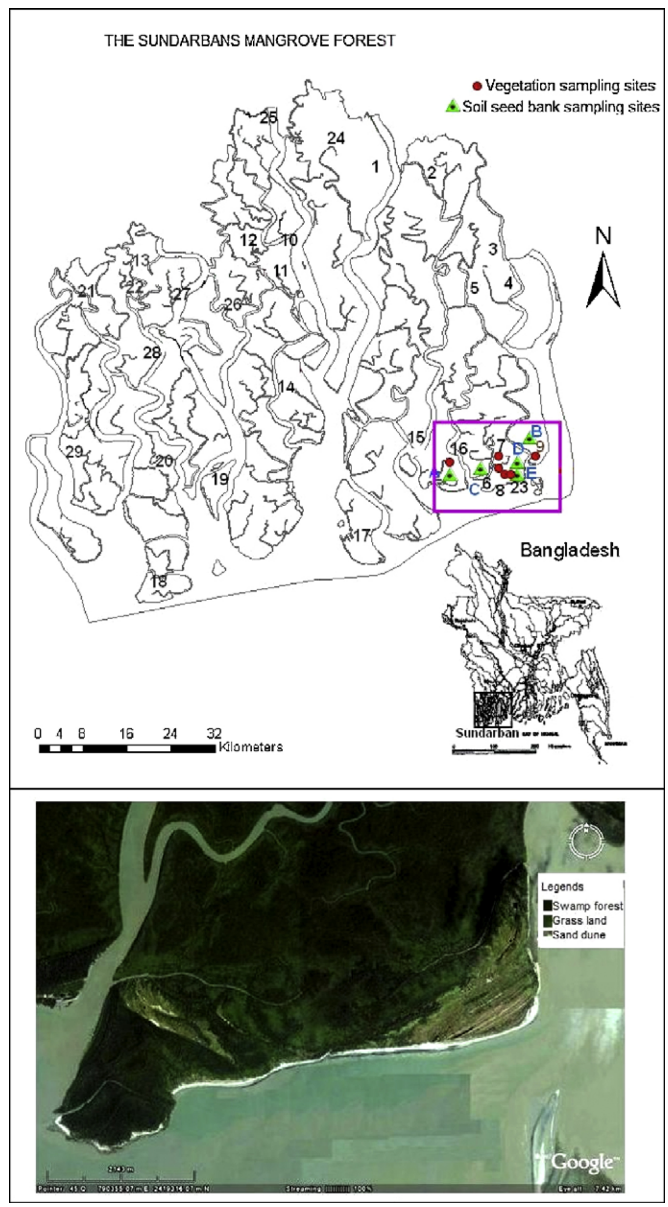

Fig. 1. Map of the study area. The inset Google™ satellite images show the habitats (dark = swamp forest dominated by mangroves, light = show grasslands and grey and white = sand dunes).

zone (Das and Siddiqi, 1985), because of the proximity of the Bay of Bengal, this area also experiences high tidal actions and high salinity (Rashid, 2007). Erosion and accretion combined with tidal surges lead to large scale variation in habitats within the mangrove forest (Rashid, 2007). Our study focused on three habitat types (Table 1): (i) swamp forests, which receives regular tidal flooding twice a day, (ii) grasslands, i.e., raised land occupied by grasses; this area usually does not receive regular tidal flooding but it receives periodic flooding during high tides and (iii) sand dunes, raised land facing seawards. General vegetation and environmental parameters of the Sundarbans mangrove forests are described in Biswas et al. (2007), Iftekhar and Saenger (2008), Karim (1988) and Rashid (2007).

2.2. Sampling protocol

We identified all three habitats of the Katka-Kochikhali delta on maps and consulted with the local forest department for validation. Then, within each habitat type, we placed our quadrats randomly using a random number generator. We followed the species area curve to determine quadrat size and used 10 m × 10 m quadrats for swamp forests and 5 m × 5 m quadrats for grasslands and sand dunes. Following this protocol, we sampled 40 quadrats in the swamp forest, 40 quadrats in the grasslands and 20 quadrats in the sand dunes. The unbalanced sampling design was due to logistical constraints. For a balanced design, we needed to sample grasslands and sand dunes either in another forest delta or in some habitats affected by human interference. However, by choosing sites within one delta, we controlled the landscape level variation and also the potential variation due to anthropogenic activities. Within each quadrat we recorded all the plant species encountered and visually estimated their percentage cover. Our first author (SHR) identified all the plant species and collected sample specimens that were further verified and preserved at the Bangladesh National Herbarium (BNH), Dhaka. We followed the protocols of Tomlinson (1986) and Jayatissa et al. (2002) for nomenclature.

Secondly, for the soil seed bank study, we selected four random quadrats from the swamp forest (out of 40), four quadrats from the grasslands (out of 40) and two quadrats (out of 20) from the sand dunes. Within each of the selected quadrats we collected two soil cores for detailed seed bank analysis. Therefore, our total soil seed bank sample of soil cores was 40 (i.e., 16 from the swamp forest, 16 from grassland and eight from the sand dune). In the same quadrat, but at a different location within the quadrat, we sampled soil cores twice: in 2004 (January–February) and in 2005 (March–April). We used a PVC soil corer (diameter 8.7 cm) for collection of soil samples at a depth of 10 cm from the soil surface. This resulted in a total soil volume of 297 cm^3 per soil core, i.e., per sample.

2.3. Seed bank analysis: germination chamber and green house experiment

After the collection of soil cores from the forest, all soil samples were stored in the laboratory, with temperatures maintained above the freezing point. Shortly after, they were processed and analyzed at the Hohenheim University, Germany.

We divided each soil sample into two halves. The first half was placed in a germination chamber. We sieved the soil samples using 0.5–2 μm sieves and separated the coarse seeds. The separated seeds were then placed inside a double layer of filter paper and sorted within a plastic box in the germination chamber at a temperature of ~17 °C to 23 °C, with aeration. We watered them as required. Many species possess tiny seeds and it was likely that they may have passed through the sieves. Therefore, we also placed the sieved soils in the germination chamber and watered them. These sets were treated at different temperature regimes ranging from ~8 °C to 35 °C, because, in a preliminary assessment of seeds mixed with soil, some seed showed germination success in a thermal gradient of 8 °C to 35 °C.

The second half of the soil sample was directly placed in the greenhouse without any sieving. We transferred the soil sample into small pots and watered them. All small pots were placed within a big tray. The greenhouse temperature was maintained between 20 ± 3.35 °C during the night and 30 ± 2.15 °C in the day time.

After a week, we observed germination both in the separated seeds and in the soil mixtures. We counted the number of germinated seedlings and identified them at 2-day intervals. This phase of the experiment continued for 6 months. While calculating species richness and density in a soil sample, we pooled germination results from the germination chamber, i.e., seeds that were directly placed and in soil mixtures and germination results from the greenhouse (Fig. 2A). For correct identification of the seed bank species, all the germinated seedlings were grown until they flowered (Fig. 2B). Thus, we transferred all the germinated seedlings from the germination chamber to the greenhouse. The full experiment in the greenhouse continued for 18 months.

2.4. Statistical analyses

In order to test whether species richness of the soil seed bank and aboveground vegetation differed significantly between three habitats, we conducted two separate non-parametric Kruskal–Wallis tests because of unequal replicates and violation of normality assumption, using habitat types as the grouping variable and species richness as the test variable. Quadrat sizes were unequal (i.e. 25 m^2 and 100 m^2). Therefore, we performed

Table 1
Habitat characteristics of the study area[a].

Micro-habitats	Salinity	Inundation[b]	Soil depth	Physical properties				Soil reactions		
				Sand (%)	Silt (%)	Clay (%)	OM (%)	pH	EC (mS/cm)	CEC
Swamp forest	32 to 45 ms/cm	Daily inundation 0 .5 m to 1.5 m	I (1-15 cm)	29.75	39.60	30.60	1.76	7.50	39.60	181
		(during winter months) and more	II (16-30 cm)	30.25	25.85	43.90	1.28	7.65	35.60	209
		than 3.5 m (during rainy season)	III (31-50 cm)	28.90	32.15	38.95	0.95	7.75	34.65	198
Grassland	17 to 39 ms/cm	Daily inundation 0.5 to 1.5 m in	I (1-15 cm)	13.15	27.15	59.70	3.90	6.95	9.10	301
		winter months and 1 to 3 m	II (16-30 cm)	14.80	32.95	52.25	1.21	7.70	7.15	286
		during rainy season	III (31-50 cm)	32.60	19.95	47.45	0.60	8.45	6.20	164
Sand dune	5 to 10.4 ms/cm	Daily inundation 0.5 to 1 m in	I (1-15 cm)	54.40	30.90	14.70	1.38	7.60	39.30	291
		rainy season and hardly any	II (16-30 cm)	80.20	13.40	6.40	0.38	8.10	23.60	268
		inundation in the winter months	III (31-50 cm)	95.30	2.70	2.00	0.27	8.20	17.70	164

[a] These are instant measurements during the study period. See Rashid (2007) for detailed methods and analytical protocol.
[b] The inundations reported here did not consider periodic fluctuations, during full-moon or no-moon, or fluctuations during extreme events.

Fig. 2. Soil seed bank species in the Sundarbans mangrove forest. (a) Seeds of halophytic grass (*Cyperus* spp.), (b) rare seeds of *Sonneratia apetala* found only in two soil cores, (c) germinated seeds in the germination chamber and (d) seedlings growing from the soil seed banks. Photo credit: M. Kruse (A and B) and R. Bocker (C and D).

necessary conversions and expressed them on a uniform scale, i.e. species richness/100 m^2, before statistical comparison.

Secondly, to test if the composition of soil seed bank species differed between habitats (i.e., dissimilarity), we ran a multiple response permutation procedure (MRPP) test. MRPP is a non-parametric test that resembles parametric discriminate function analysis. MRPP is flexible over unequal sample sizes and violation of normality assumptions (McCune and Mefford, 1999). MRPP compares the average distances (dissimilarity) within a group with the average distances resulting from all the other possible combinations of the data set. The test statistic delta is the average of the observed within group distances weighted by their relative group size. The observed delta is compared to the possible deltas resulting from Monte Carlo permutations of sample observations to the groups. Based on the frequency distribution of random deltas, the test calculates the probability of the observed delta given the null hypothesis of no group difference. We used Euclidean distance to calculate dissimilarity and ran 1000 permutations to calculate the p value. Similarly, another MRPP was conducted to analyze the dissimilarity in the aboveground vegetation between the three habitats.

Thirdly, to test for similarity in the soil seed bank and the aboveground vegetation, we conducted three separate Mantel tests for three different habitats. For this comparison we used aboveground vegetation data for only those quadrats where we sampled the seed bank. This allowed us to compare directly the similarity in aboveground vegetation and the seed bank. The Mantel test uses two distance matrices, i.e., dissimilarity matrices to test the null hypothesis of no relationship among them. The Mantel result is expressed as a correlation coefficient r. We used aboveground vegetation (presence–absence) data in the first matrix and soil seed bank (also presence–absence) in the second matrix. To calculate dissimilarities, we used the Bay-Curtis distance for both matrices. Unlike MRPP, the Mantel test also calculate p values based on the possible r (Mantel statistic) resulting from Monte Carlo permutations of sample observations to the groups. We ran 999 permutations to calculate the p value. We performed all the analyses in SPSS version 16 (SPSS, 1999) and Pc-Ord version 5.11 (McCune and Mefford, 1999).

3. Results

Species richness in the aboveground vegetation differed significantly between the three habitats (Kruskal–Wallis, $\chi^2_{df=2} = 74.98$, $p < 0.001$). The largest number of species was observed in the grasslands, followed by swamp forests and sand dunes (Fig. 3A). MRPP showed a significant difference in species composition between the three habitats (MRPP test, $p < 0.001$, Fig. 4A). Swamp forests were dominated by mangrove species (e.g., *Excoecaria agallocha*, *Ceriops decandra*, *Heritiera fomes*, *Nypa fruticans*, etc.) while grasslands and sand dunes were dominated by grasses and sedges with sporadic occurrence of a few mangrove species (*Phragmites karka*, *Imperata cylindrical*, *Sporobolus tremulusa*, *Acrostichum aureum*, *Acanthus ilicifolius*, etc.) (see Table 2).

We identified 23 species from the soil seed banks. Most of them were non-mangrove species, including halophytic herbs, mangrove associate species, salt-tolerant grasses and sedges (Table 3). Surprisingly, we found two true mangrove species, i.e., *Sonneratia apetala* and *Sonneratia caseolaris* in the soil seed bank. The three habitats differed significantly in the soil seed bank species richness (Kruskal–Wallis test, $\chi^2_{df=2} = 23.27$, $p < 0.0001$). Sand dunes supported the largest number of soil seed bank species, followed by swamp forest and the grasslands (Fig. 3B). However, the three habitats did not differ significantly in species composition (MRPP test, $p = 0.319$, Fig. 4B). Grasslands and sand dunes were mostly dominated by grasses, sedges and some herbaceous species, while the soil seed bank in the swamp forest consisted predominantly of grasses (Table 3).

In the grasslands and sand dunes, aboveground vegetation is similar to the species composition of the soil seed bank (Mantel test, for grasslands, $r = +0.22$, $p = 0.22$; for sand dunes, $r = -0.20$, $p = 0.177$). In the swamp forest, the aboveground vegetation was highly dissimilar from the soil seed bank species (Mantel test, $r = -0.13$, $p < 0.05$).

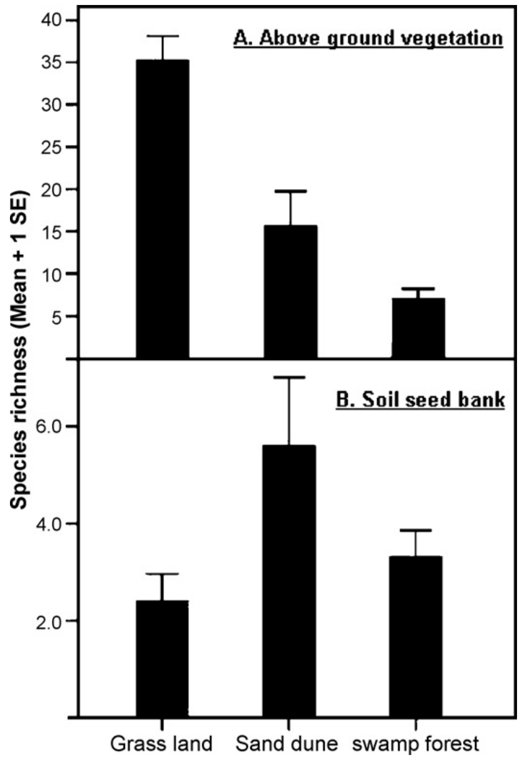

Fig. 3. Species richness of the aboveground vegetation and the soil seed bank species in the three habitats within the mangrove. For the aboveground vegetation richness is expressed as # of plant species/100 m^2 and for the soil seed banks that is the # of plant species/soil core, i.e. 297 cm^3.

4. Discussion

4.1. Variations in the soil seed banks and persistence of the grasslands within mangrove habitat

While the composition of the aboveground vegetation differed between habitats, the soil seed bank species did not differ. This may be explained by the availability of propagules and/or a favorable microclimate for survival and/or establishment of those propagules. According to the tidal sorting hypothesis (Rabinowitz, 1978), mangrove propagule availability and vegetation zonation is regulated by tidal actions with an interaction of propagule size. Sand dunes are exposed to the coast and experience the most severe tidal actions and are unstable. Swamp forests are next to the sand dunes along a tidal gradient from the sea shore to the forest interior, whereas the grasslands are open areas within the protected belt of swamp forests. Therefore, despite the fact that sand dunes receive the largest number of mangrove propagules, most of them cannot become established due to a lack of suitable substrate and frequent tidal disturbance. Secondly, the swamp forest canopy is mostly closed. Therefore, light demanding species cannot establish unless there is a large canopy gap (Das and Siddiqi, 1985). If the size of the gaps are small, as is usually the case due to tree mortality, then that gap would not be suitable for grassland formation, but for colonization of late successional mangrove species such as *Heriteria fomes*, *Excoecaria agallocha* and *Bruguiera gymnorhiza*. This is one of the typical successional pathways in the Sundarbans mangrove forests (*sensu* Das and Siddiqi, 1985) and gap regeneration in mangroves (Clarke and Kerrigan, 2000). If the size of the gaps, i.e., canopy openings, are large, as is the case after severe cyclonic or catastrophic events, then that gap may be suitable for grassland formation for two reasons. First, these habitats are protected by swamp forests and at higher elevation positions. Secondly, because of the large canopy openings, light demanding species and species that are non-recalcitrant and persist in the soil seed bank can easily become established. Common mangrove grasses possess this trait. Once these species are established, they will act as a barrier (hedge) for the arrival of large sized mangrove propagules (Biswas et al., 2007). Therefore, grasslands persist for long time within the mangrove habitat as an alternate stable state and develop their own soil seed banks. As a feedback, seeds from grasslands can also disperse back to the swamp forest, not only by a reverse tide but also by wind and herbivores (Dolon, 2003). Many of these seeds remain dormant in the soil seed bank, for example, we found many grasses in the soil seed banks of the swamp forest (Table 3). The non-persistence of mangrove species in the soil seed banks is due to their non-persistent traits such as vivipary, crypto-vivipary and recalcitrant seeds (Fransworth, 2000).

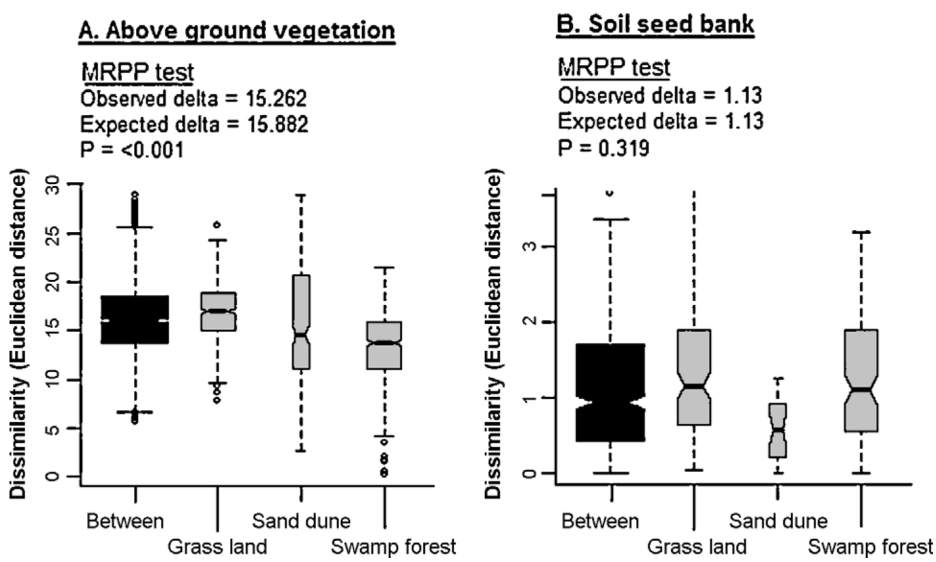

Fig. 4. Dissimilarity (between and within) in the composition of aboveground vegetation (A) and the soil seed bank species (B) in relation to the three habitats.

Table 2
Aboveground species composition in the three habitats within the Sundarbans. N.B. Only dominant species are shown.

Swamp forest		Grassland		Sand dune	
Species	Abundance	Species	Abundance	Species	Abundance
Excoecaria agallocha	26.61	*Phragmites karka*	53.79	*Borassus flabellifer*	62.55
Ceriops decandra	20.03	*Imperata cylindrical*	34.54	*Syzygium fruiticosum*	14.17
Heritiera fomes	6.05	*Sporobolus tremulus*	28.93	*Porteresia coarctata*	13.79
Nypa fruticans	6.05	*Stenochlaena palustris*	21.72	*Pandanus foetidus*	5.68
Cynometra ramiflora	2.51	*Calotropis gigantea*	15.71	*Saccharum spontaneum*	4.83
Cerbera manghas	2.51	*Clerodendrum inerme*	15.40	*Clerodendrum inerme*	2.55
Derris trifoliate	2.50	*Phoenix paludosa*	14.06	*Tamarix indica*	2.55
Erythrina variegate	2.50	*Ceriops decandra*	11.26	*Erythrina variegate*	2.53
Eugenia fruticosa	2.50	*Acrostichum aureum*	10.26	*Caesalpinia bonduc*	2.50
Flagellaria indica	2.50	*Acanthus ilicifolius*	4.45	*Eugenia fruticosa*	2.50
Hibiscus tiliaceus	2.50	*Erythrina variegate*	2.55	*Leea crispa*	2.50
Lepisanthes rubiginosa	2.50	*Clerodendrum viscosum*	2.50	*Streblus asper*	2.50
Phragmites karka	2.50	*Ipomoea pes-caprae*	2.50	*Phragmites karka*	2.21
Brownlowia tersa	2.32	*Saccharum spontaneum*	2.50	*Ipomoea pes-caprae*	2.00

4.2. Recovery of mangrove vegetation after catastrophic disturbance

After severe habitat disturbance, the availability of incoming propagules from an adjacent forest stand becomes limited. The availability of propagules from an adjacent stand would depend on phenological events such as fruiting/seeding time of the mangrove species. If the disturbance event occurs shortly before or after the fruiting season, the possibility of recovery by mangrove species is high because of the immediate availability of mangrove propagules. Alternatively, if the catastrophic disturbance event occurs in an off fruiting/seeding time because of the lack of dispersed propagules and favorable microhabitats, such as canopy openings, soil seed bank species that are mostly non-mangrove and mangrove associate species could establish in the vacant habitats. Our results also concur with this prediction since we found no significant difference in the soil seed bank and aboveground vegetation in the open grasslands (Mantel test, $p = 0.22$).

Table 3
Soil seed bank species (mean # of seeds/m^3) in the swamp forest, grassland and sand dunes within the Sundarbans mangrove forest of Bangladesh. Invasive species (*sensu* Biswas et al., 2007) are shown in bold face.

Species	Habitats		
	Swamp forest	Grassland	Sand dune
Acrostichum aureum L.	**34.50**	**15.85**	**11**
Alternanthera sessilis R.Br.	–	0.60	–
Amaranthus viridis L.	–	0.85	–
Bacopa moniera (L.) Pennei.	0.70	3.40	–
Ceratopteris thalictroides (L.) Brongn.	1.45	14.25	–
Cyperus difformis L.	1.75	10.5	6.12
Cyperus brevifolius C.B. Clarke	1.85	3.05	1.45
Cyperus kyllinga Endl.	–	7.25	–
Cyperus scariosus R.Br.	1.25	7.75	18.80
Cyperus spp.	0.35	1.70	–
Chenopodium ambrosioides L.	–	2.05	–
Crinum asiaticum Lour.	–	0.75	–
Derris trifoliata Lour.	**1.85**	**16.50**	**2.85**
Fimbristylis ferruginea (L.) Vahl	–	5.40	15.15
Fimbristylis spp.	–	0.78	–
Imperata cylindrica (L.) P.Beauv.	–	0.76	–
Leersia hexandra SW.	–	1.35	0.36
Pentagramma triangularis (Kaulfuss) Maxon.	1.95	5.62	–
Phyla nodiflora (L.) Greene.	–	0.85	–
Pycreus sanguinolentus Beauv.	1.75	6.75	–
Sporobolus tremulus Kunth.	2.05	–	–
Sonneratia apetala Buch.-Ham.	0.56	–	–
Sonneratia caseolaris (L.) Engl.	0.56	–	–
Unidentified	1.84	2.10	–

The majority of mangrove species produce their fruit/seeds during the monsoon season (Troup, 1921) that is also the peak time for tropical cyclones and storms (Rashid, 2007). Therefore, propagules often remain available after cyclonic events and forests can recover. In recent years, however, due to climate change, the intensity and frequency of tropical cyclones have increased (Houghton et al., 2001; Solomon et al., 2007). Many of these catastrophic events are now occurring during the off fruiting/seeding season, e.g., the Asian tsunami in 2004 and cyclone Sidar in 2007, causing an immediate removal of mangrove propagules. The unavailability of mangrove propagules and vegetation cover results in opportunistic invasive and non-mangrove species, e.g., salt-tolerant grasses and mangrove associate species to cover the vacant space quickly. The opportunistic invasive and non-mangrove species are mostly disturbance tolerant and have their viable propagules in the soil seed bank. In the mangrove forest of the Sundarbans this type of large scale invasion by non-mangrove and mangrove associate species is quite common now, especially towards the sea shore such as near Katka-Kochikhali and Hironpoint (S.R. Biswas, *personal observation*). These areas are locally known as non-commercial covers (NCCs), as defined from a management perspective. Several authors (e.g. Biswas et al., 2007; Iftekhar and Saenger, 2008) expressed their concern over the recent increase in NCC lands in the Sundarbans.

In both of our discussed pathways of vegetation recovery after a catastrophic disturbance, mangrove habitats become occupied by vegetation, either of functional mangrove species or non-mangrove and mangrove associate species. This latter pathway is known as cryptic ecological degradation (Dahdouh-Guebas et al., 2005). Dahdouh-Guebas et al. (2005), after studying ancient Sri Lankan mangroves, found that, although there was no reported change in the mangrove areas, the composition of functional mangroves was changed due to changes in the hydrologic regime. Although thorough studies are not available for the mangrove forests of the Sundarbans in Bangladesh, it can be assumed that there might be an increasing trend of cryptic ecological degradation—increasing abundance of non-mangrove and associated mangrove species. After analyzing 30 years of inventory data, i.e., with commercial and dominant species only, Iftekhar and Saenger (2008) showed that there was a marginal decrease of the dominant mangrove species *Heriteria fomes* while some of the salt tolerant and disturbance specialist species, such as *Excoecaria agallocha*, *Ceriops*, increased their area of occupation. The increasing occupancy of *Excoecaria agallocha* may be due to their disturbance tolerance ruderal strategy (Tomlinson, 1986) while the increasing occupancy of non-mangrove and mangrove associate species may be due to their persistence in soil seed banks.

4.3. Persistence of invasive species in the soil seed bank

Biswas et al. (2007) identified 23 invasive plant species in the mangrove forests of the Sundarbans. We found two of these very abundant invasive species in the soil seed bank (see Table 3). The persistence and abundance of invasive species in the soil seed bank is of serious concern (Richardson and Kluge, 2008), when considering their management and eradication. From our field observations and those of Biswas (2003) it was also evident that in many areas of the Sundarbans, especially towards the sea shore, such as Dimer *char* and Pakhir *char*, invasion of *Derris trifoliata* has already appeared as problematic. Future study may focus on the expansion of invasive species over a temporal scale.

4.4. Caveats

Several assumptions are associated with our findings and should be taken into account during interpretation of our results. First, we conducted this study within the southeastern part of the Sundarbans only. Aboveground species composition, including the dominant vegetation is different in two other ecological zones of the Sundarbans, such as the saline and brackish water zones (Das and Siddiqi, 1985). Therefore, findings of this study may not be applicable to the mangroves of the Sundarbans as a whole. Future studies should focus on the soil seed bank species richness and composition differences in a salinity gradient. Secondly, we collected soil samples twice; pre-monsoon and during the monsoon season. Although these are the peak times for most mangrove propagule dispersal, some species produce fruits and disperse at other times of the year (Troup, 1921). Although our soil sampling during the monsoon and post-monsoon period accounted for most of the mangrove soil seed banks and because this is the dispersal time for most of the mangrove propagules, an ideal study should take account of year round activities, given the fact that mangrove seeds are recalcitrant in nature (Fransworth, 2000).

5. Conclusion

Our study confirms the widely accepted notion that mangrove species do not possess a persistent soil seed bank (*sensu* Fransworth, 2000; Ungar, 2001) while mangrove seed banks are occupied by mangrove associate species, invasive species and many non-mangrove species. These findings have major implications for the management of mangrove forests of the Sundarbans. The current management regime in the Sundarbans mangrove forest relies only on natural colonization, thus there is no plantation activity. Because of global environmental changes, unusual events, especially catastrophic events, are occurring more frequently. This leaves a very limited time frame for mangrove vegetation recovery after a particular catastrophic event. We have discussed how persistent non-mangrove species, mangrove associate species and invasive species could lead towards cryptic ecological degradation and biological invasion after those catastrophic disturbances. Therefore, we suggest that instead of relying only on natural regeneration, forest managers should actively consider plantation of mangrove species in the larger canopy gaps created after catastrophic disturbances.

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