Increasing habitat loss and human disturbances in the world's largest mangrove forest: the impact on plant-pollinator interactions

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Abstract

The Sundarbans, the largest mangrove forest in the world and a UNESCO world heritage site has been facing an increasing pressure of habitat destruction. Yet, no study has been conducted to test how human disturbances are affecting plant-pollinator interactions in this unique ecosystem. Hence, our aim was to provide the first study of the impact of habitat loss and human disturbances on plant-pollinator interactions in the Sundarbans. We selected 12 sites in the North-Western region of the Sundarbans, along a gradient of decreasing habitat loss and human activities from forest fragments near human settlements to continuous pristine forest, where we studied insect pollinators of two mangrove plant species, *Acanthus ilicifolius* and *Avicennia officinalis*. Our results show that different pollinator groups responded to the disturbance gradient differently. The abundance of *Apis dorsata* increased gradually from the village area towards the deep pristine forest. On the other hand, *A. cerana* and *A. florea* were found in the village sites and completely absent in the deep forest. Although pollinator community composition changed along the disturbance gradient, their efficacy in pollination did not seem to be significantly affected. However, lower plant diversity and low understory plant cover in the forest patches nearby the village indicated that the high anthropogenic activities not only affected pollinator community composition but also played a major negative role in the regeneration of the forest. Our study provides first insights into plant-pollinator interactions in the Sundarbans and demonstrates that more research is needed to inform conservation of this unique habitat.

Key words: conservation, mangroves, the Sundarbans, pollination, *Acanthus ilicifolius, Avicennia officinalis, Apis cerana, Apis dorsata, Apis florea*

Introduction

Human destruction of natural habitats and alteration of landscapes are considered as major drivers of the world-wide forest loss and fragmentation (Aizen and Feinsinger, 1994; Fischer and David, 2007; Haddad et.al, 2015). This increasing disturbance and habitat loss not only change the distribution and abundance of different organisms but also affect species interactions, which may be amplified into long-term effects on the forest ecosystem (Fortuna and Bascompte, 2006). Plant-pollinator interactions play a crucial role in ecosystem function as around 90% of angiosperm species rely on pollinators at least to some extent for their sexual reproduction (Ollerton *et al.* 2011, Potts *et al*. 2016). This makes pollinators an essential component to maintain the biodiversity and ecosystem integrity (Kearns *et al*. 1998; Potts *et al*. 2003).

Alterations of natural habitats can affect plant-pollinator interactions in different ways. On the one hand, pollinators can be affected by the lack of suitable habitat and resources, which may determine their performance (Ward and Johnson, 2005). On the other hand, decreased plant abundance, density and health will result in lower pollen availability leading to reduced seed set for plants (Ward and Johnson, 2005). From the pollinators' perspective, destruction of habitats is expected to reduce species richness, abundance and homogenize species composition (Steffan-Dewenter & Westphal, 2008, Biella et al. 2019, 2020). Furthermore, increased flight distance among habitat fragments can cause less effective pollen transfer (Aizen and Harder 2007). Pollinator abundance can also decrease due to lower attractiveness of isolated fragments, small population size, or reduced density of flowering plants (Cheptou and Avendano, 2006). Overall, the stability of plant-pollinator interactions tends to be altered when native habitat is changed or removed. Even small disturbances may cause disruption of plant–pollinator interactions within the remaining habitat patches in fragmented landscapes (Keitt, 2009).

Unlike most terrestrial ecosystems, mangroves are naturally fragmented, architecturally simple and often have limited species diversity, but with a number of uniquely adapted species (Vannucci, 2001, Alongi, 2002). Heavily populated coastal zones have accelerated the widespread clearing of mangroves for coastal development, aquaculture, or other resource uses (Polidoro *et al*., 2010) and have led to further forest destruction, fragmentation and habitat loss. Globally, around 20%- 35% of mangroves have been lost since 1980s and approximately 1% of the mangrove areas are disappearing per year (Valiela *et al*. 2001; FAO, 2003; FAO, 2007). An extreme example of forest loss and habitat destruction is the Sundarbans mangrove forest, situated in the south-western Bangladesh, which is the world's largest continuous mangrove forest (Sarkar *et al*., 2016). Nearly 50% of the forest has been lost since the 1950s because of inadequate habitat protection, and large-scale habitat alteration (Feller *et. al.,* 2010). Historical human pressures have severely degraded the Sundarbans ecosystem by depleting forest tree stock (Ellison *et. al*., 2000) and causing habitat loss. Despite the numerous ecosystem services provided by mangrove forests (Walters *et al.*, 2008), very little is known about pollinator communities in the mangroves (Pandit and Choudhury, 2001; Hermansen, *et.al*., 2014), and there have been no studies in the Sundarbans. Not only habitat loss, but also introduction of non-mangrove plants in the forest, either intentionally or accidentally, and keeping honeybees (mainly *Apis cerana*) for apiculture along the forest edge to increase honey production are sources of concern about the maintenance of biodiversity in this mangrove forest.

With increasing concern about the future of this mangrove forest, this study is the first attempt to assess the pollinator communities in the Sundarbans and the impact of increasing human pressure on the plant-pollinator interactions. Therefore, we addressed three questions: i) Does the plant diversity and abundance of floral resources vary with the increasing human disturbances? ii) Does the abundance or composition of the pollinator community change along the gradient of human impact? iii) Do differences in pollinator visitation along the gradient have consequences for pollination and seed production of selected mangrove plants?

Methods

Study area

This study took place in the North Eastern part of Sundarban Mangrove Forest in Bangladesh, located nearby Munshigang, Shyamnagar, Satkhira (N 22°16'78, E 89°11'58). The Sundarbans is protected as a UNESCO world heritage site. There are three protected sites in this forest in the

Bangladesh sites of the Sundarbans: East Wildlife Sanctuary (ES, 312 km2), South Wildlife Sanctuary (SS, 370 km2), and West Wildlife Sanctuary (WS, 715 km2) (Gopal and Chauhan, 2006).

However, the part of the forest we studied is outside of these protected areas and highly disturbed by human activities and facing a high rate of biodiversity loss. The forest is distinctly isolated by the river Pankhali from the adjacent human settlements, though fragmented forest patches are still found inside the village areas.

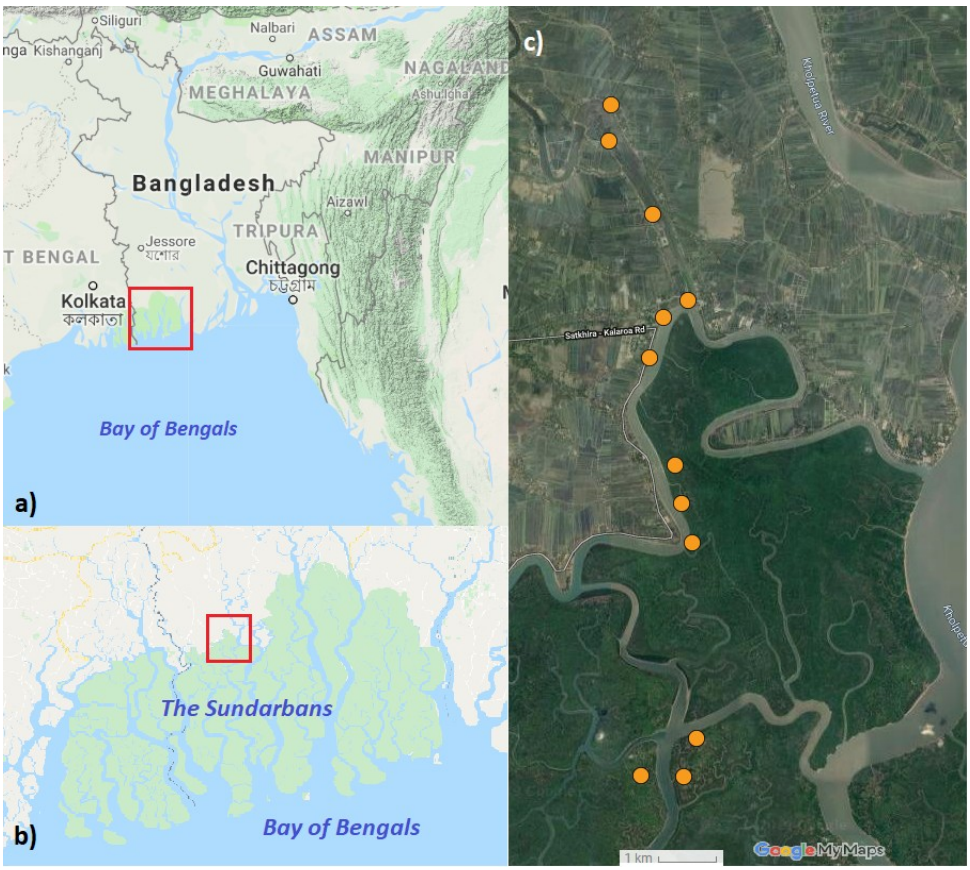

Fig 1: Location of the study area and the position of individual sites. Location of the Sundarbans mangrove forest in Bangladesh (A.) and location of our study area at the inland edge of the mangrove forest (B.). Location of individual sampling sites in the village and forest area (C.). Map data: Google, Imagery: TerraMetrics.

Based on the distance of isolated forest patches from the forest, canopy and ground cover and intensity of human disturbances, we selected twelve sites (Fig. 1C, site characteristics:). Therefore, our study sites expanded from the most fragmented and isolated forest patches in the village to the pristine forest sections and from the most to the least affected by anthropogenic activities. The maximum distance from the most disturbed site to the least disturbed site was ca. 10 km. Forest patches inside the village were adjacent to the high-density human settlement and completely exposed to their daily life activities. The grounds of these sites had no or very little understory vegetation and distance from the continuous forest was 1-2.5 km. Forest patches which were close to the river, were also exposed to high human activities and had little understory vegetation as well. On the other hand, sites on the opposite side of the river in the continuous forest with moderate human impact had around 50 % ground covered by understory plants. Finally, forest patches which

were deep in the forest and the farthest from the village, were least or not disturbed at all, high in plant density and almost fully covered by the herbaceous and shrub plants (Data: https://doi.org/10.6084/m9.figshare.11877615). This part of the forest is only occasionally visited by the forest department and the collectors of honey from wild *Apis dorsata* colonies.

Plant diversity assessment

We surveyed the vegetation of all sites during our field work. We identified all the species in each site and estimated total canopy cover, cover of the understory layer, and percentage cover by individual plant species. Only two plant species were flowering at all sites the time of our study. Hence, these two species were chosen for a detailed study.

***Acanthus ilicifollius* L.** (Lamiales: Acanthaceae) is an evergreen, non-viviparous, semi-woody spiny shrub, which grows up to two meters. It has a wide range of distribution; it occurs from Western India through the North-Eastern China to Southern Australia (Tomlinson, 1986). This species is very important for the accumulation of soil sediments and stabilization of the ground in brackish water areas. Inflorescence is spike, terminal, flower is large, showy, light blue to purple coloured, contains one large petal, four stamens, is bisexual and semi-tubular in shape (Aluri *et al*, 2017). The species produces nectar and pollen, has a mixed breeding system where out-crossing plays the most important role and it was reported to be pollinated by large bees (Raju, 1990). Flowering time in the Sundarbans spans from April to June but can be different for other parts of its distribution zone (Ramasubramanian *et al*., 2003, Upadhyay and Mishra, 2010). Fruit is a capsule containing up to four seeds which disperse by effective anemochory especially during the dry season (Raju *et al*., 2017).

Figure 2: The target plant species of our study. *Acanthus ilicifolius* plant and flower (left); *Avicennia officinalis* plant and flower (right). Photo: Asma Akter.

***Avicennia officinalis* L.** (Lamiales: Acanthaceae) is a common viviparous mangrove tree, which has a wide range of distribution from Southern India through Indo-Malaya, to New Guinea and the Eastern Australia (Tomlinson, 1986, Duke 1991). It is a medium-sized tree, typically twenty meters tall, but can be up to thirty meters tall and contains pneumatophores. Inflorescence is spike, flower is small, yet the largest among the *Avicennia* species, orange-yellow coloured with four petals, four stamens, bisexual, open (Aluri, *et al*., 2012). It produces both nectar and pollen, is self-compatible

although it is protandric, has a long flowering period suggesting its adaption for cross-pollination, and is mostly pollinated by bees and flies (Aluri, *et.al.*, 2012). Flowering time is from April to August, depending on the location. Flowering is triggered by the rain and may vary even over a short distance (Opler *et. al*, 1976; Reddy *et al.*, 1995). Like other *Avicennia spp*., *A. officinalis* contains 4 ovules but in general only one ovule develops into mature seed, which is non-dormant and germinates while fruit is still attached to the tree, thus are crypto-viviparous in character (Tomlinson, 1986, Raju, *et.al.*, 2012).

Insect sampling

We observed and sampled flower-visiting insects form the two locally most abundant plant species, *Acanthus ilicifolius* and *Avicennia officinalis*. We surveyed them in May-June 2018, during the peak flowering time. We conducted our observations and sampled floral visitors for ten days. In each site, we sampled for 20-30 minutes in each session, replicated six times, which resulted into 120-160 minutes of observation for each species per site. During the high tide a vast area of the forest is flooded, and this occurrence restricted our fieldwork to 4-6 hours per day (Data: https://doi.org/10.6084/m9.figshare.11877615). For our observations we set up three collection windows with a size of 1 m^2 for each plant species and we always sampled in the same windows. For both species we counted the number of inflorescences and number of flowers per inflorescence within the window. For the *Avicennia officinalis*, we also measured the total flower cover in each window. We had three windows in every site for both species. Insects were observed and collected by netting, from 7 a.m. to 5 p.m., in sunny and warm condition, no observation were made under rain, storm or high winds. We determined the flower visitors when they touched the reproductive parts of the flower or entered the flower with tubular shape. Insect samples were stored in the freezer after the collection and later mounted and stored dry in boxes for identification.

Stigma collection and pollen tubes analysis

We collected stigmas at the end of our fieldwork to determine the impact of pollinator efficacy for each plant. Stigmas were collected from 30 flowers per site excluding the plants where pollinators were observed. Only those stigmas where the female phase was over and no longer receptive were collected. Collected stigmas were stored in Formalin-Acetic-Acid solution (FAA) at room temperature. To assess the pollen tube growth, stigmas were softened and stained by following the technique of Martin (1959). Stigmas of both species were softened in 1M NAOH for 24 hours. After softening, stigmas were stained with 0.1% Aniline blue in 0.1M K_2HPO_4 for 15 hours in the dark. After completing staining, stigmas were washed and mounted in 50% Glycerine drop on glass slide and covered with cover slips for observing under the fluorescence microscope and pollen tubes were counted. All the processes were done at room temperature and after the observations, samples were stored in 4°C for future reference.

Fruit and seed collection

Fruits were only collected from *Acanthus ilicifolius* from each site. Fruiting of *Avicennia officinalis* in that area occurs during July-August, which is at the peak of the rainy season, when the forest is inaccessible and fruit collection was thus not feasible. Fruit production of *Acanthus ilicifolius* was assessed as the number of fruits collected per inflorescence (3-12 inflorescences per site) and seed production was estimated by counting the number of seeds per fruit in each inflorescence. The number of seeds per fruit ranges from zero up to four in a fully seeded pod.

Statistical analysis

Shannon's Diversity Index (Shannon, 1948) was used to compare plant and pollinator species diversity between the sites. We analysed the impact of the position of the sites along the gradient from highly disturbed to the least disturbed parts of the forest (expressed as the distance of the sites from the village in km) on plant abundance and diversity using generalised linear models (GLM). We used Gaussian error distribution for plant species richness and Shannon's diversity index, and binomial error distribution with overdispersion ("quasibinomial") for proportion plant cover. Multiple values of flower abundance, insect visitation, and pollen grains deposited on stigmas were measured repeatedly at each site, so we used generalised linear mixed-effects model (GLMM) with site identity as a random factor and Poisson error distribution for these response variables. We also used the duration of the observation period and the number of flowers in the observation window (both log-transformed) as an offset in the GLMM of insect visitation to properly analyse variation in visitation per flower per hour (Reitan & Nielsen, 2016). We analysed fruit and seed production in *A. ilicifolius* using similarly constructed GLMMs, with the number of flowers in an inflorescence used as an offset (log-transformed) when analysing the number of fruits per flower, and the number of fruits used as an offset (log-transformed) when analysing the number of seeds per fruit. We used R 3.4.4. (R Core Team 2018) for all analyses and plots; GLMMs were fitted using the lme4 package (Bates et al. 2015).

Results

Plant diversity and abundance

Overall, we found 13 plant species of 9 families in the sampled sites (Data: https://doi.org/10.6084/m9.figshare.11877615). However, more plant species can be found in the wider area.

We observed the lowest plant species richness and diversity in the forest patches nearby the village (Fig. 3A and 3B), which were dominated by mostly *Sonneratia apetala* Buch.-Ham., *Excoecaria agallocha* L., and *Avicennia officinalis* L., all of them tree species. Plant species richness and diversity increased along the gradient from the village towards the undisturbed forest interior (GLM, F=6.4, P=0.030 for species richness, and F=4.5, P=0.060 for Shannon's diversity index). *A. ilicifolius* was the only shrub plant in the forest patches in the village area. The understory plant cover increased significantly towards the forest interior (GLM, F=29.6 , P=0.0003; Fig. 3D), unlike the canopy cover (GLM, F=3.4, P=0.096; Fig. 3C)

We also estimated the plant cover individually for our two target plant species and counted the number of flowers/m^2 for both plant species to assess their floral abundance. Plant cover of the shrub *A. ilicifolius* gradually increased from village towards the forest interior (GLM, F=56.3, P<0.0001; Fig. 4A) but did not change significantly in the tree *A. officinalis* (GLM, F=0.32 , P=0.58; Fig. 4B). Flower density of *A. ilicifolius* did not vary significantly along the gradient (GLMM, X^2=0.95 , P=0.33; Fig. 4C), while *A. officinalis* showed decreasing flower density from village towards the deep forest (GLMM, X^2=8.9 , P=0.0029; Fig. 4D).

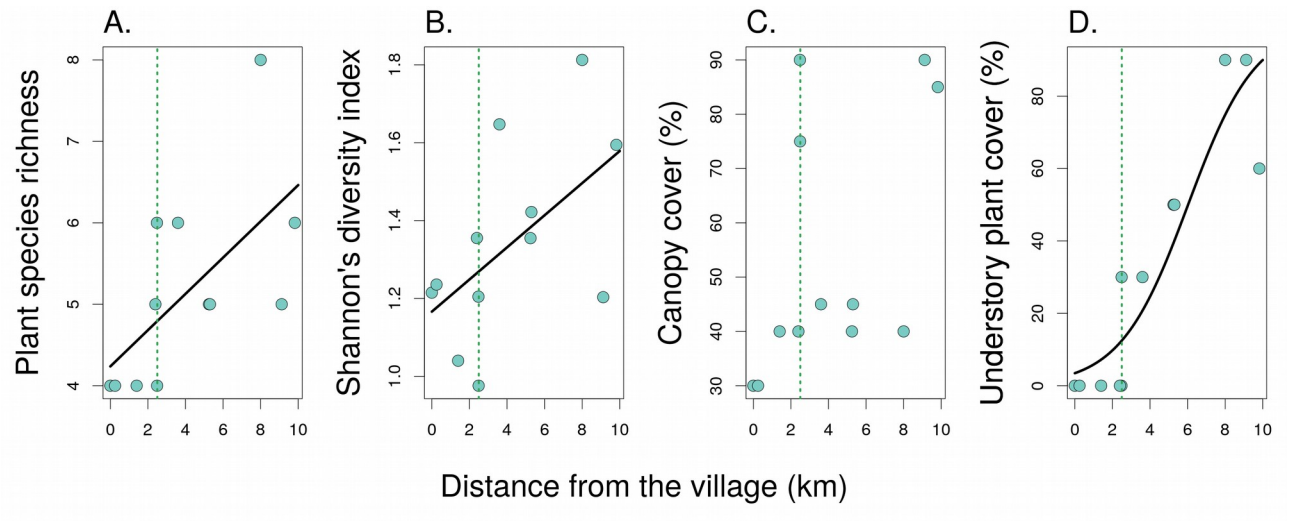

Figure 3: Plant diversity and abundance along the disturbance gradient and distance from the village towards the pristine forest: plant species richness (A.), Shannon's diversity index (B.), canopy cover (C.) and understory plant cover (D.) for each site.

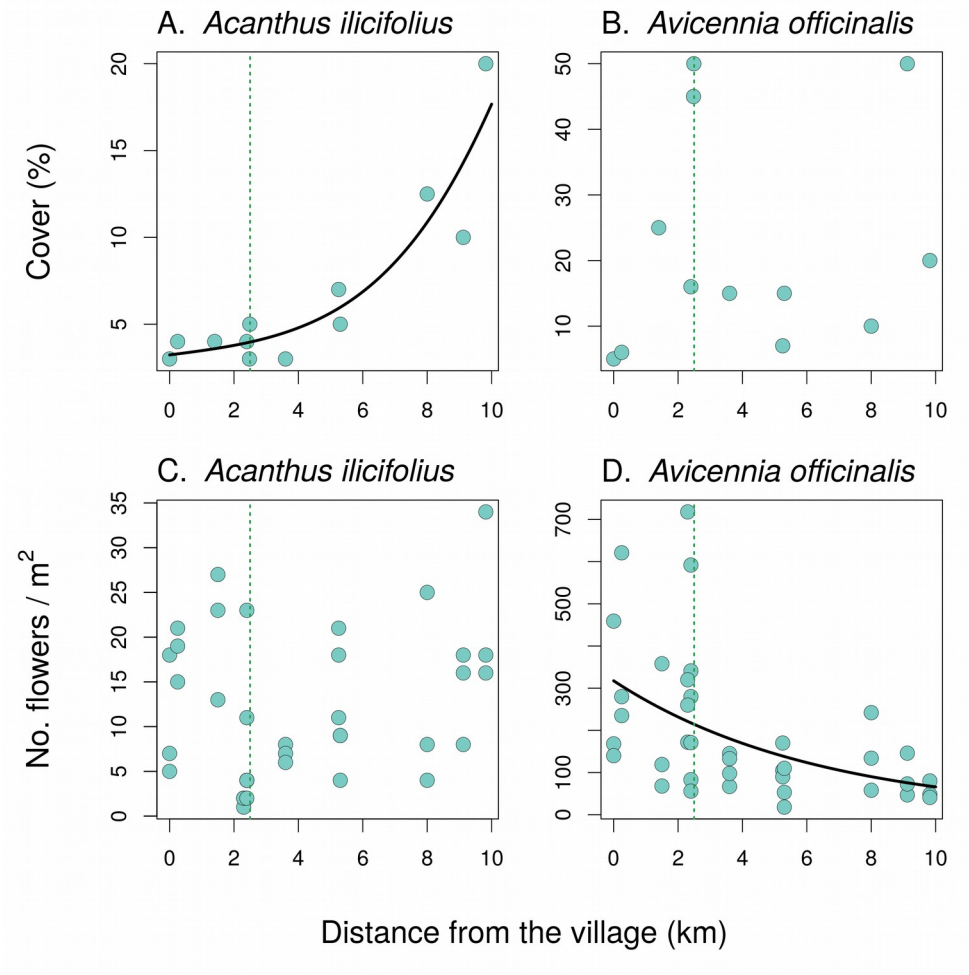

Figure 4: Individual plant cover and number of flowers for two target species: **A.** Plant cover for *A. ilicifolius* (shrub). **B.** Plant cover for *A. officinalis* (tree). **C.** Flower abundance for *A. ilicifolius* and **D.** Flower abundance for *A. officinalis*. X-axis showing the distance of the sites along the gradient from the village towards the undistrubed forest interior (**A**-**D**).

Insect diversity and flower visitation rate

Flower visitor community in our sampling period of this part of the forest consisted of the major insect groups, such as Hymenoptera, Diptera, Coleoptera and Lepidoptera. We observed and sampled in total 4431 pollinating insects sorted into 103 morphospecies, where bees made up to 80% of the total number of pollinator individuals. Among the bees, around 50% of them belong to the genus *Apis*. *A. dorsata* Fabricius, 1793, also known as the giant honey bee, was the most abundant overall both in the village and forest. Additionally, *Apis cerana* Fabricius, 1793, the eastern honey bee or the Asiatic honey bee, and *Apis florea* Fabricius, 1787, the dwarf honey bee, were found in the forest patches near the village, but were completely absent in the deep forest. Other significant bee groups were *Xylocopa* spp. and solitary bees. Among the non-bee pollinators, flies and beetles made up to 15% of the total pollinators.

We found no significant changes in the total visitation of the two plant species by pollinators along the gradient from the village to the undisturbed forest interior (GLMM, X^2=1.5, P=0.22 for *A. ilicifolius*, and X^2=2.8, P=0.096 for *A. officinalis*). In addition, there was no significant change in morphospecies richness of pollinators along the gradient for both plant species (GLM, F=0.49, P=0.050 in *A. ilicifolius* and F=1.4, P=0.26 in *A. officinalis*). The Shannon's diversity index of the pollinator community also did not change in *A. illicifolius* (GLM, F=2.1, P=0.17) and *A. officinalis* (GLM, F=1.5, P=0.25). However, species composition of the pollinators varied, with some species or groups dominant in the village area and others in the forest interior (Fig. 5, Fig. 6, Table 1).

Table 1: Visitation rate by different groups of pollinators on the two plant species. Results of statistical tests (GLMM) of the changes of the visitation rate by insect orders and individual species of honey bees along the disturbance gradient from the village towards the forest interior. Likelihood ratio test was used to test the statistical significance of each fitted relationship.

	Acanthus ilicifolius			***Avicennia officinalis***		
Insect order	**slope**	**X^2**	**P**	**slope**	**X^2**	**P**
Hymenoptera	0.06	1.37	0.2419	0.11	3.15	0.0758
Diptera	-0.10	4.40	**0.0359**	-0.08	0.49	0.4828
Coleoptera	0.26	4.43	**0.0353**	0.31	7.56	**0.0060**
Lepidoptera	-0.26	0.98	0.3227	-0.19	0.11	0.7420
Honey bee species						
Apis dorsata	0.34	13.56	**0.0002**	0.24	11.54	**0.0007**
Apis cerana	-0.52	5.31	**0.0212**	-0.41	13.42	**0.0002**
Apis florea	-0.50	6.85	**0.0089**	-1.21	6.90	**0.0086**

Both plants were visited mostly by Hymenoptera at a rate which did not vary along the disturbance gradient, while the visitation rate by Diptera on *A. ilicifolius* decreased and visitation rate by Coleoptera increased along the gradient on both plants (Table 1). Lepidoptera were observed rarely and mostly at sites along the edge of the continuous portion of the forest (Fig. 5). Composition of the insect community based on the morphospecies data changed significantly along the disturbance gradient (RDA, F=2.7, P=0.011 in *A. ilicifolius* and F=3.0, P=0.0024 in *A. officinalis*). The three honey bee species of the genus *Apis* were the most frequent visitors on flowers of both plants, but

they responded differently to the disturbance gradient (Fig. 6). *A. cerana* and *A. florea* abundances decreased with the distances of forest patches from the village towards the forest, while the number of *A. dorsata* increased gradually with the increasing distances of forest patches from the village (Fig. 6).

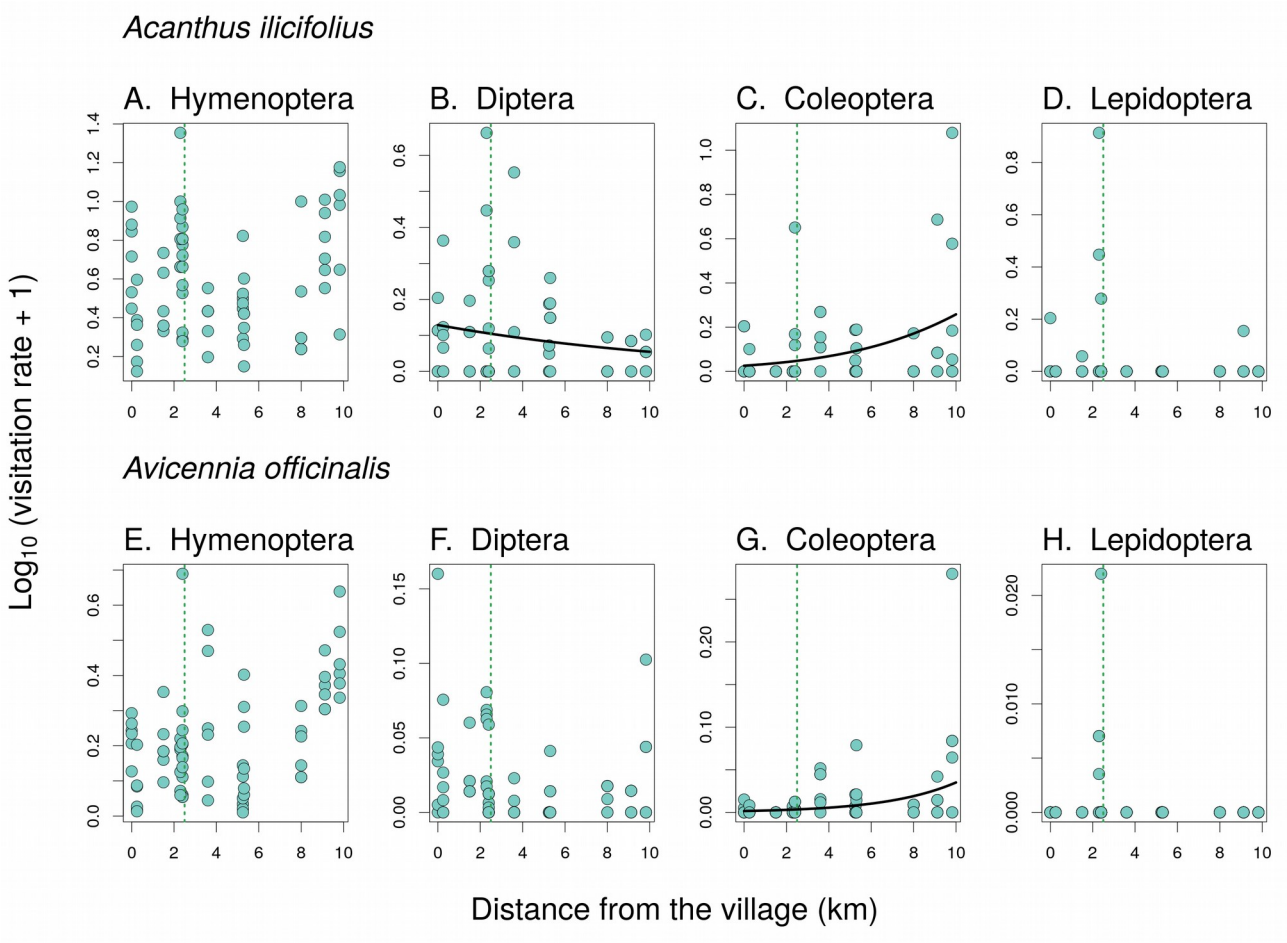

Figure 5: Visitation rate of insect orders on the two plants. The number of visits per flower and hour on *Acanthus ilicifolius* (A. - D.) and *Avicennia officinalis* (E. - H.). The estimated relationship is plotted as a line only in cases where it was statistically significant according to a likelihoo ratio test (see Table 1). The vertical dotted green line shows the point along the disturbance gradient where the continuous forest begins and continues further away from the vilage.

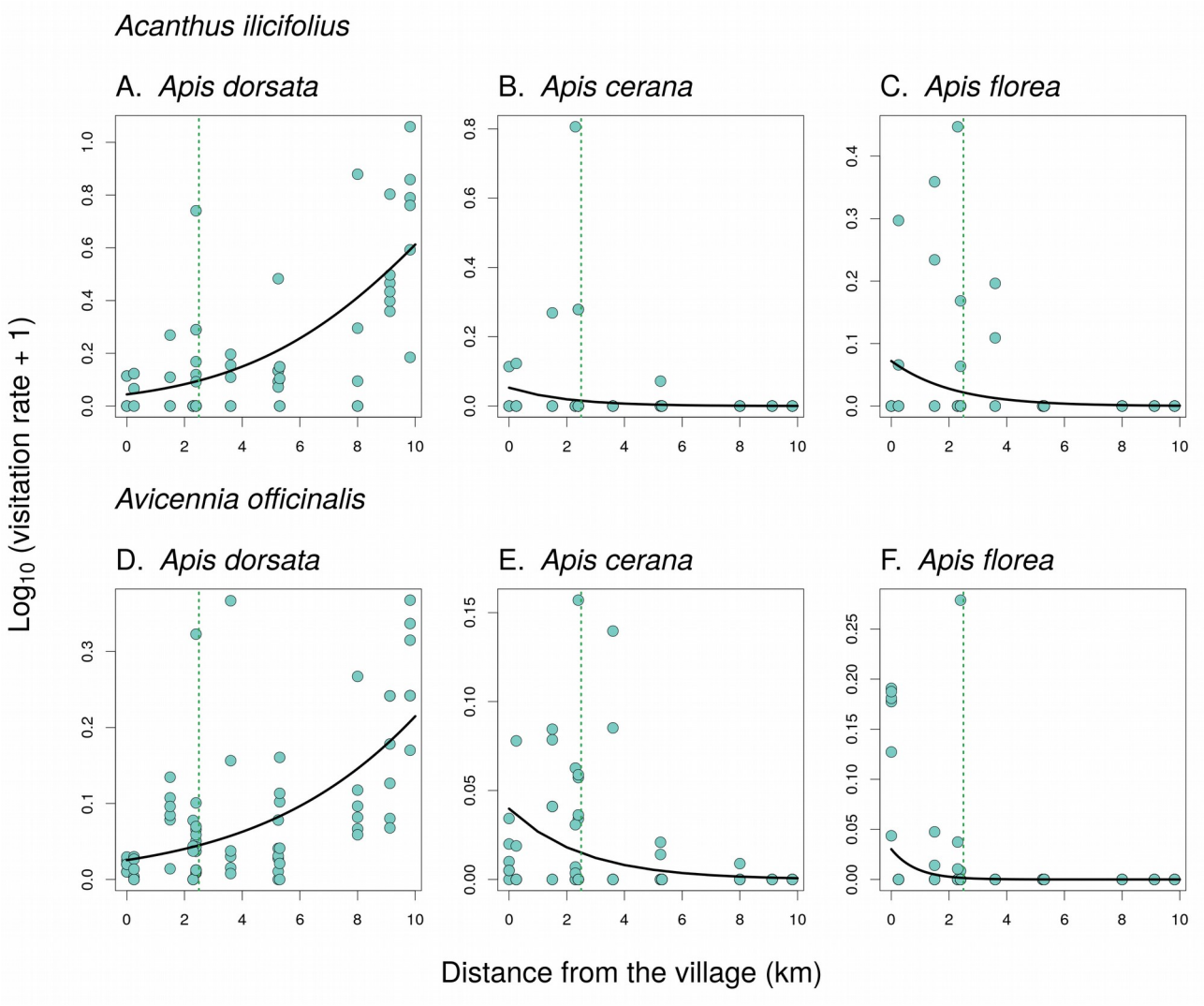

Figure 6: Visitation rate of the three species of honey bees on the two plants. The number of visits per flower and hour on *Acanthus ilicifolius* (A. - C.) and *Avicennia officinalis* (D. - F.). The relationship between the visitation rate and distance from the village was statistically significant in all cases according to a likelihood ratio test (see Table 1). The vertical dotted green line shows the point along the disturbance gradient where the continuous forest begins and continues further away from the village.

Pollen deposition and seed production

Although we observed significant variation in the composition of pollinator communities of both plants along the disturbance gradient from the village to the forest interior, pollination was not highly affected by these variations. The number of pollen tubes in the *A. ilicifolius* did show a significant increase in the total number of pollen grains deposited on its stigmas with the distance from the village towards the forest interior (GLMM, X^2=4.2, P=0.041; Fig. 7A), but this did not translate into differences in fruit and seed production. That is, the number of fruits per inflorescence was not affected by the distance along the gradient from the village towards the forest interior (GLMM, X^2=0.29, P=0.59), the same holds for the number of seeds per fruit (GLMM, X^2=0.069, P=0.79). The second species, *A. officinalis*, showed no differences in the total number of pollen grains deposited per flower along the disturbance gradient (GLMM, X^2=1.3, P=0.25; Fig. 7B), while seed set data were not available.

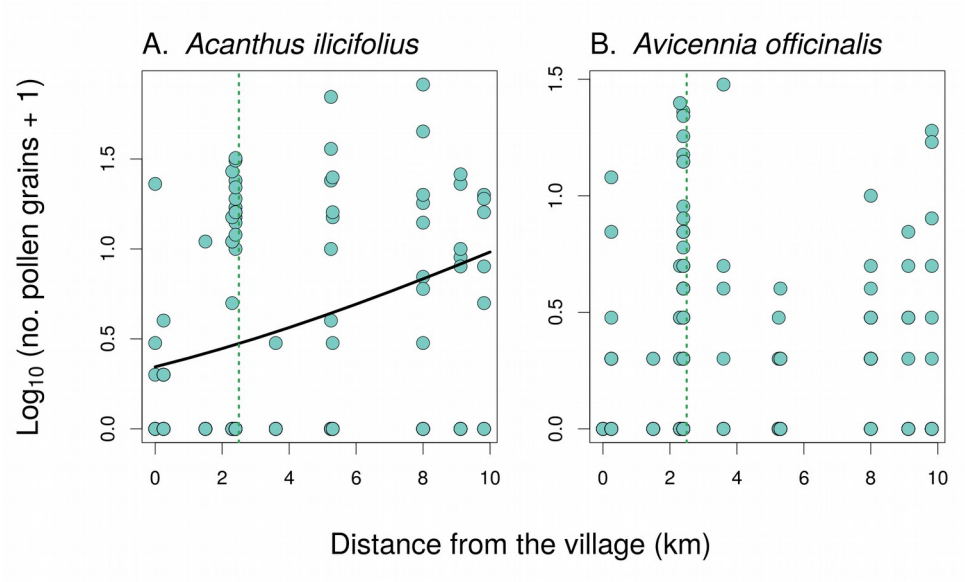

Figure 7: Pollen deposition on stigmas of the two plant species. The number of pollen grains deposited on stigmas of *A. ilicifolius* (A.) and *A. officinalis* (B.) in relation to the distance from the village towards the forest interior. The relatioship was statistically significant only in *A. ilicifolius*. The vertical dotted green line shows the point along the disturbance gradient where the continuous forest begins and continues further away from the vilage.

Discussion

Our study area was located in one of the most threatened parts of the Sundarbans mangrove forest, a UNESCO world heritage site, in terms of increasing pressure of human population, urbanization, landscape alteration and anthropogenic activities (Ghosh *et al*., 2016). These factors are gradually affecting the forest structure and function in various ways. So far, no attention has been directed towards understanding how the increasing human pressure affects interactions of native mangrove plants with their pollinators. Our research shows changes in the plant community structure, the composition of the pollinator communities, and flower visitation patterns along the gradient of decreasing human disturbance from a village area towards a relatively pristine forest interior.

Impact on plant diversity

This part of the mangrove forest showed lower plant species richness compared to other less disturbed areas of the forest (Polidoro *et al*., 2010). Moreover, forest patches nearby the village had the lowest number of plant species and the lowest values of the Shannon's diversity index. These fragmented forest patches near villages were used by the local people as grazing land for their domestic animals and plant leaves and stems were regularly collected for fuel and fodder. All these activities led these forest patches having almost no understory, only bare ground under the trees, and very low plant species richness and diversity. Another important reason for the lack of understory in patches closer to the village is that local villagers cut the understory to deter tigers, as they prefer to hide in the bushes for hunting (Badhwar, 1988). Furthermore, pollutants from boats and households may hamper the regrowth of plants in such forest patches (Santos *et al*., 2012).

Like the overall plant diversity, the abundance (percentage cover) of *A. ilicifolius* was lower in the patches nearby the villages and increased significantly towards the deep forest interior. Being an

understory plant, this species was highly disturbed by the animal grazing resulting in lower cover. Although plant cover increased with the distance from the village, flower production per unit area did not show any differences. The percentage cover of the other target species, *A. officinalis,* did not show any change in relation with the anthropogenic activities, but its flower abundances decreased towards the deep forest. This can be due to the rain deficiency in this part of the forest as *Avicennia* species flowering time shows a high sensitivity to rainfall (Opler *et.al*., 1976; Reddy *et.al*., 1995) or due to the increasing salinity as several study showed delayed flowering in plants due to the increasing salinity (Maas and Poss, 1989, Khatun *et al*. 1995). This forest is lying in the Bay of Bengal delta and with the advantage towards the deep forest from village leads to higher salinity as sea gets closer (Haque and Reza, 2017). We point out that *A. officinalis* had an unusually high cover in some of the patches at the transition between the village and continuous forest. These patches were partially planted by the forest department (Rahman and Rahman, 2015) to support the restoration of the forest. *A. officinalis* is one of the most common plants which are used in mangrove plantation (Saenger and Siddique, 1993).

Effect on flower visiting insects

The most abundant flower visitors of both target plant species were three species of honey bees of the genus *Apis*. The giant honeybee (*A. dorsata*, not domesticated) was the major pollinator in every site. We found that *A. dorsata* abundance increased sharply from the village towards the forest interior. Although *A. dorsata* was reported to be a vital pollinator for both cultivated crops and wild plants (Robinson, 2012), they usually forage in more abundant flower resources and may be a poorer competitor than the other two *Apis* species (Koeniger and Vorwohl, 1979). Additionally, despite of their long-distance foraging ability, *A. dorsata* tend to forage close to their nest if the flower resources are abundant (Punchihewa *et.al.*, 1985). This may explain why their abundance is lower in forest patches nearby the village and higher in the deep forest, where most of their hive can be found. Furthermore, forest patches nearby the village are more exposed to both professional and non-professional honey collectors and naturally occurring *A. dorsata* hives are disturbed, extracted and even destroyed by the honey-collectors more frequently. The collection of honey likely led *A. dorsata* to have low number of hives in the areas of the forest close to the village, which resulted into lower flower visitation rates by *A. dorsata*.

Another important *Apis* species, *A. cerana* is completely domesticated. Beehives of *A. cerana* maintained by local beekeepers were located mostly at the edge of the continuous forest and therefore they were able to forage both in the forest and village patches within their foraging distance (Partap, 2011). However, they foraged more in the village area, possibly because of higher availability of floral resources. Finally, the dwarf honey bee, *A. florea*, which is not domesticated, had a distinct habitat preference compared to *A. cerana*. *A. florea* was only found in those forest patches which were closest to the village, where their hives were located. This species was never found in any of the sites inside the continuous part of the forest. It is possible that this is because the mangrove forest only offers abundant flower resources for a limited time, only from March to June, and many non-mangrove plant species are available year around in the village area, which makes these sites more suitable for this smaller bee.

Unlike in *Apis* spp., the disturbance gradient had little effect on the total flower visitor abundances and at the level of insect orders only Coleoptera increased towards the forest interior on both plant species. The morphospecies composition of the flower visitor communities changed along the gradient, but we lack detailed information about the biology of individual species apart from *Apis* spp. discussed above.

Impact of anthropogenic activities on pollination

Although our study showed that there was a difference in the pollinator communities among the sites from village to forest, we found no effect on the pollination of the flowering plants in terms of fruit production. But the plant diversity and abundance were highly variable between the patches nearby the village and deep forest. Also, high number of beehives of domesticated *A. cerana* may have affected the *A. dorsata* abundance near the village. This scenario showed that the exposure of the forest patches to the human activities have negative impact on plant and pollinator communities, but the fruit production did not get affected by the presence of *A. cerana* and *A. florea*. Mangrove forest is dependent on the bee pollination and similarly mangrove provides an excellent forage for bees (Lacerda, 2002). Additionally, different studies on the *Apis* species stated that these three species can co-occur without any significant competition (Punchihewa, *et al*., 1985, Oldroyd, *et al*., 1992, Koetz, 2013). Furthermore, *A. dorsata* is a well-known migratory pollinator and according to the locals most of them move out from the Sundarbans after the major flowering season (March-June). During monsoon and before their return to the forest, pollination is mostly done by the solitary bees in the forest and other *Apis* species in the village areas. Studies in other low-land forest areas in Asia showed that *A. dorsata* immigrates in the mass flowering season and when the amount of floral resources drop, they leave the forest (Nagamitsu, 1998; Itioka *et al.*, 2001). In contrast, the resident *Apis* species and other solitary bees, stay year around and pollinate the flowers in general (Sakai, 2002). Hence, keeping domestic honey bees in the mangrove areas is widely accepted as not harmful from the conservation point of view. However, interactions between the domesticated *A. cerana* and other pollinators are not well-known. A number of recent studies on European honeybees *Apis mellifera* showed their strong negative effects on wild pollinators (Magrach *et al.* 2017, Henry & Rodet 2018, Hung *et al*. 2019). Exploring the interactions between the Asian honeybees *A. cerana* and wild pollinators in similar detail will thus be an important topic for future research.

Perspectives for forest conservation

The Sundarbans, the largest continuous mangrove forest in the world, is facing an increasing threat of deforestration and forest degradation. The impacts on both plant and animal diversity are likely to be severe, therefore, we need to focus on developing sound conservation policies for this mangrove forest. Based on our result from pollen deposition and seed production, it seems that changes in the composition of the pollinator community did not affect the pollination success greatly, but still the plant diversity and cover was significantly lower in patches close to the village. This suggests that, despite the successful pollination and seed production, human exploitation interrupts forest regeneration and likewise affects the pollinator community.

Moreover, overexploitation of giant honey bees, *A. dorsata,* was likely responsible for lower abundance of this species in forest patches near the villages. Continuous destruction of its nests and habitat may lead to further decline of the giant honey bee in this area. Local extinctions of *A. dorsata* have been reported across their vast distribution range (Oldroyd and Nanork, 2009) and deserve attention regarding their conservation. In addition, more intensive research will be needed to decide whether keeping domestic beehives in this area is beneficial or harmful for the local pollinator communities and plant diversity. We also need to gain a better understanding of the diversity and functional role of non-bee pollinators in the mangroves.

To conserve the affected areas of forest, it is necessary not only protect them form disturbances but also initiate more intensive conservation approaches, e.g. mangrove tree plantation. The closer the forest patches to the human settlement, the more vulnerable they are. Hence, it is necessary to

increase awareness about the necessity of forest conservation among the locals and involve them directly in forest conservation. Understanding the importance and long-term benefits of conservation would be the key to protect this forest.

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