Exotic Species Invasion and Biodiversity in Bangladesh Forest Ecosystems

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Summary

Both, biological invasion by exotic plant species and biodiversity including spatial patterns and drivers are two major issues in tropical forest ecosystems. This dissertation deals with these two issues in a tropical forest ecosystem in Bangladesh. Considering the first issue, it comprises two manuscripts: a systematic review and a field survey in Bangladesh forest ecosystem.

The review was done based on a formalized literature search in order to summarize the approaches that were hitherto applied as well as to mark gaps in tropical invasion research. A considerable number of primary research papers focused on invasion by plants in tropical forests were reviewed. The results identified ample gaps of research. Adressing these gaps may generate promising future research to understand and mitigate this great challenge in different types of tropical forests.

Then a case study was conducted to examine the invasiveness and invasibility characteristics in a forest ecosystem of Bangladesh. This study seeks to find out the characteristics of exotic species and relationships between native species richness, environmental variables, disturbances and exotic plant invasion in this ecosystem. Boosted Regression Trees and Detrended Correspondence Analysis are used to determine these relationships. Most exotics are trees followed by shrubs and herbs. Fabaceae and Asteraceae contribute a large proportion of exotic species. Most of them originated from other tropical areas. Native species richness was found to be the best predictor for the number and percentage of exotic species in the study area. However, a unimodal relationship was found. Multiple other factors also influence the success of exotic species. The number and the percentage of exotic species are positively correlated with frequency of disturbances and with soil attributes (phosphorus and bulk density) but negatively correlated with topography (elevation) and conservation patterns (protection).

Considering the biodiversity issue, it encompases another two manuscripts based on a case study conducting a systematic field work in the same forest ecosystem of

Bangladesh. They are the first spatially explicit analysis of drivers and patterns of biodiversity in this terrestrial ecosystem based on multivariate approaches, similarity analysis and variation partitioning. One manuscript assesses the relationships between landscape and habitat characteristics, conservation patterns, and plant diversity in this tropical forest ecosystem. This study analyses the effects of soils, topographic conditions, disturbances and nature protection on plant species richness and species composition. The results reveal that biodiversity patterns in the study area are positively correlated with protection and elevation. These patterns are, however, negatively correlated with disturbances.

The other manuscript focuses on the stand characteristics and spatial patterns of biodiversity as they are rarely studied in the tropics in general and in Bangladesh in particular. Data on tree species are used as they are the most conspicuous element of these ecosystems. Tree species composition was recorded in a systematic plot design and diameter was measured at breast height for each individual tree. Distance-decay approach was applied to analyze the spatial pattern of biodiversity for the whole study area and two subsamples from Satchari National Park and Satchari Reserve Forest. Analyses showed that biomass increased significantly with protection status. Plots in the Reserve Forest were associated with higher species turnover than in the National Park.

This dissertation identifyies, for the first time in a systematic approach, the major drivers for invasion and biodiversity pattern in a forested area in Bangladesh. In conclusion, both, biological invasion by exotic plant species as well as biodiversity are strongly related to the disturbance regime and nature protection.

Zusammenfassung

Zwei der bedeutendsten Aspekte der Erforschung tropischer Wälder sind zum einen die biologischen Invasionen durch exotische Pflanzenarten und zum anderen die Biodiversität mit ihren räumlichen Ursachen und Mustern. Diese Dissertation behandelt beide Themen am Beispiel eines tropischen Waldökosystems in Bangladesch. Der erste Aspekt wird in zwei Manuskripten untersucht: Einer systematischen Literaturstudie sowie einem Fallbeispiel in einem Waldökosystem in Bangladesch.

Die formalisierte Literaturstudie fasst die bisher angewandten Forschungsansätze zusammen und zeigt bestehende Lücken der Invasionsforschung in den Tropen auf. Eine nennenswerte Anzahl an Forschungsarbeiten zur Invasion von Pflanzen in tropischen Wäldern wurde begutachtet. Die Ergebnisse weisen auf große Forschungsdefizite hin. Eine Bearbeitung dieser Lücken kann vielversprechende Forschungsarbeiten hervorbringen, welche zum Verständnis und zur Lösung der großen Herausforderungen in verschiedenen tropischen Waldsystemen beitragen können.

In der Fallstudie wurde anschließend untersucht, welche Eigenschaften in einem Waldökosystem in Bangladesch zu einer erhöhten Invasibilität beitragen. Diese Studie erarbeitet verschiedene Charakteristika exotischer Arten und untersucht deren Zusammenhang mit Artenreichtum, Umweltvariablen und Störungen. Die Analyse wurden mittels „Boosted Regression Trees" und Korrespondezanalysen (Detrended Correspondence Analysis) durchgeführt. Bei den meisten nicht heimischen Arten handelt es sich um Bäume, gefolgt von Sträuchern und krautigen Pflanzen. Die Neophyten gehören zu einem großen Teil zu den Fabaceae und Asteraceae und stammen meist aus anderen tropischen Gebieten. Im Untersuchungsgebiet stellt die Anzahl heimischer Arten den besten Prädiktor für Anzahl und prozentualen Anteil exotischer Arten dar. Der Zusammenhang kann durch eine parabelförmige Kurve charakterisiert werden, jedoch beeinflusst eine Vielzahl anderer Faktoren den Erfolg nicht heimischer Arten. Anzahl und Anteil exotischer Arten korrelieren positiv mit der Frequenz der Störungen und Bodeneigenschaften (Phosphor und Schüttdichte), jedoch negativ mit der Topographie (Höhe ü. NN.) und dem Naturschutzstatus.

In Hinblick auf Fragestellungen zur Biodiversität umfasst diese Dissertation zwei weitere Manuskripte, die auf Feldstudien im selben Waldökosystem in Bangladesch basieren. Es handelt sich dabei um die erste räumlich explizite Analyse der Ursachen und Muster der Biodiversität in diesem terrestrischen Ökosystem. Sie verwendet multivariate Statistik, Ähnlichkeitsanalysen und Varianzpartitionierung. Eines der Manuskripte untersucht den Zusammenhang zwischen Landschafts- und Habitat-Charakteristika, sowie dem Naturschutz und der Pflanzenvielfalt in diesem Ökosystem. Sie analysiert den Einfluss von Boden, topographischen Bedingungen, Störungen und Naturschutz auf Pflanzenvielfalt und die Vergesellschaftung von Pflanzenarten. Die Ergebnisse verdeutlichen, dass die Biodiversitätsmuster im Untersuchungsgebiet stark positiv mit dem Naturschutzstatus und der topographischen Höhe korrelieren, aber einen negativen Zusammenhang mit Störungen zeigen.

Das zweite Manuskript richtet seinen Fokus auf Bestandeseigenschaften und räumliche Muster der Biodiversität, da diese sowohl in den Tropen als auch in Waldökosystemen Bangladeschs selten untersucht werden. Verwendung finden Daten zu Bäumen, da dies die bedeutendsten Elemente dieser Ökosysteme darstellen. In einem systematischen Aufnahmedesign wurden Baumartenzusammensetzung und Brusthöhendurchmesser jedes Individuums gemessen. „Distance-decay“ Analysen wurden auf das gesamte Untersuchungsgebiet sowie auf zwei verschieden stark geschützte Teilbereiche angewandt. Dabei wurde eine signifikante Zunahme der Biomasse mit dem Naturschutzstatus beobachtet. Der räumliche Artenumsatz ist in den weniger geschützten Bereichen des Schutzgebietes größer als in der Kernzone.

Diese Dissertation erarbeitet erstmalig systematisch die bedeutendsten Ursachen für Invasions- und Biodiversitätsmuster in Wäldern Bangladeschs. Schlussfolgernd kann gezeigt werden, dass sowohl biologische Invasionen durch exotische Pflanzenarten, als auch die Biodiversität stark mit Störungsregimen und dem Naturschutz zusammen hängen.

Introduction

Concept of invasion and its effects

In the last decades, it has been highlighted in various fields of research (e.g. ecology, environmental sciences, biogeography) and practise (agriculture, forestry, natural resource management, nature conservation) that the dispersal of non-native or alien species throughout the world is representing a leading threat to the ecosystems worldwide (Heywood, 1989; Prieur-Richard & Lavorel, 2000; Dukes, 2002; Weber, 2003; Seabloom *et al.*, 2006). Biological invasion of exotic species can have serious conservational and ecological consequences for oceanic island ecosystems as well as for the large portion of flora and fauna in continental areas (Vitousek *et al.*, 1996; Vitousek *et al.*, 1997). The rapid globalization of economies is responsible for the transportation of exotic species into new areas where they are not native especially through international travel and trade. This initial transportation induces further abundance and expansion into introduced areas (Liebhold *et al.*, 1995). This spread and introduction of alien species into new areas may happen either accidentally or deliberately. They can have impact on their introduced ranges in various ways, e.g. displacing native species, disrupting ecosystem processes (Drake *et al.*, 1989; Cronk & Fuller, 1995). However, the effect of invasion is a lasting, damaging, pervasive, widespread, and global phenomenon with serious consequences for ecological communities, economic activities, and social systems (Mack *et al.*, 2000; Pimentel *et al.* 2005; Weber, 2003).

Biological invasion has been considered as one of the most important components of global change. It is posing serious threats to the conservation of native ecosystems world-wide (D'Antonio & Vitousek, 1992; Dukes & Mooney, 1999; Lonsdale 1999; Mack *et al.*, 2000; Fine, 2002; Mooney & Hobbs, 2002; Naylor, 2002; Seabloom *et al.*, 2006). Global changes due to invasions are significant and have long-term effects. They are at least as important as other influences like changes in climate, the atmosphere, and land use because these may not be reversible in hundreds to thousands of years (D'Antonio & Vitousek, 1992). During the last 100 years, human activities, especially international travel and trade, have overcome oceanic and others natural barriers for world's biota. These anthropogenic vectors are accelerating the rate of invasion by alien species, which is catalizing the future global change (Dukes & Mooney, 1999; Lonsdale, 1999). The surpassing of biogeographic barriers is altering the ecosystem structure and function and consequently accelerating the decline in biodiversity globally (Lonsdale, 1999; Naylor, 2002).

Invasive species have been identified and observed to have hazardous effects on ecosystem structure and function or ecosystem properties and processes. They are responsible for the alteration of structural components of ecosystems e.g. induce functional and compositional change; reduce native species richness, and functional components or processes (e.g. primary productivity, decomposition, hydrology, geomorphology, nutrient cycling, and disturbance regimes) (Mack *et al.*, 2000). They are causing the extinction of vulnerable native species through herbivory, predation, competition, habitat alteration, and diseases (Vitousek *et al.*, 1997; Gurevitch & Padilla, 2004). They are threatening the existence of native species by hybridization and introgression; altering geo-morphological processes; influencing the microclimate; slowing or alteration of succession; disrupting evolutionary processes etc. (Drake *et al.*, 1989; Cronk & Fuller, 1995). Based on theory and observational data, it was found that mostly alien predators and pathogens have been responsible for the well-documented extinctions of native species (Davis, 2003).

Usually in conservation planning, the target of protected-areas has been fixed at 10% of a biome, of a country or of the planet (Brooks *et al.*, 2004). Currently, it is one of the major issues confronting management of nature reserves that invasive species are threatening plant species in the protected areas as well as making the habitat unsuitable for animals (Usher, 1988; Macdonald *et al.*, 1989; Underwood *et al.*, 2004).

Invasive species can alter the rates of resource acquisition or resource use efficiency in the ecosystems. For example, in Hawaii Volcanoes National Park, an introduced nitrogen fixing tree, *Myrica faya*, native to Canary Islands, alters the resource supply in the ecosystem substantially. It influences ecosystem development in young nitrogen-poor volcanic soils through its nitrogen-fixing attribute. It encourages future invasion offering nitrogen for other alien species (Vitousek & Walker, 1989).

Invaders can also modify the trophic structure of the invaded community through the addition or removal of top carnivores (D'Antonio & Vitousek, 1992).

Invaders can alter the disturbance regime of invaded ecosystems through changing the type, frequency, intensity and spatial extent of disturbance. This influence on disturbance regimes affects ecosystem structure and function and supports the establishment of future exotic species (Hobbs & Huenneke, 1992; Burke & Grime, 1996; Mack & D'Antonio, 1998). Sometimes, invaders themselves may act as a disturbance (Lockwood *et al.*, 2007). They can disturb the soil; increase erosion; increase biotic disturbance; increase herbivory and predation; alter habitat structures; increase competition; modify nutrient cycling, hydrology, and energy budgets; change fire cycles; and change microclimatic conditions (Mack & D'Antonio, 1998; Mack *et al.*, 2000; Lockwood *et al.*, 2007).

Invasion may affect societal ambitions such as economic growth, poverty alleviation, and food security (Naylor, 2002). For instance, the grass *Imperata cylindrica* spreaded approximately 60 million hectares of land in Asia and made these large tracts of lands infertile (Tomich *et al.*, 2001). The economic impacts of biotic invasions can be categorized into different ways. One can try to asses the value of biodiversity as well as the associated costs of species loss. They can be grouped into agricultural impacts e.g. costs of losses in crop production, reduction of production in livestock, fisheries, rangelands. They can be classified with respect to control e.g. cost of combating invasions including all forms of quarantine, control, and eradication (Mack *et al.*, 2000). Translating the impacts of invaders on biodiversity and ecosystems into economic aspects indicates large economic costs (Vitousek *et al.*, 1996; Vitousek *et al.*, 1997; Pimentel *et al.*, 2001; Seabloom *et al.*, 2006). These economic costs include indirect environmental consequences and other non-market values affected by invasive species (McNeely *et al.*, 2001).

Invasive exotic species may affect native plant populations through different mechanisms through which they dominate over native species (Elton, 1958; Crawley, 1987; Rees & Paynter, 1997; Mack *et al.*, 2000; Siemann & Rogers, 2001; Thébaud & Simberloff, 2001). Different hypotheses of invasion ecology have been formulated to explain invasion mechanisms or exotic species success in different ecosystems

(Hierro *et al.*, 2005; Catford *et al.*, 2009). One suggestion is the evolution of invasiveness hypothesis i.e. introduced exotic species undergo rapid genetic changes due to new selection pressure in a new environment (Carroll & Dingle, 1996; Sakai *et al.*, 2001; Maron *et al.*, 2004). In case of some species this mechanism can be explained by enemy release hypothesis. This means they have been released from their native specialist enemies. As a result they can reallocate more resources for their growth and production which they would have to use to resist these enemies in their native range (Darwin, 1859; Crawley, 1987; Blossy & Notzold, 1995; Davis *et al.*, 2000). The invasive neotropical shrub *Clidemia hirta*, native to Costa Rica, is a vigorous invader in tropical forests of Hawaii. It is released from its herbivores and pathogens in its introduced range. It threatens native populations being invasive through this mechanism (Dewalt *et al.*, 2004). Some exotic species may succeed through allelopathic effects. This is summarized in the novel weapon hypothesis i.e. exotics release allelochemicals in their intrduced community. These allelochemicals are relatively ineffective against well-adapted neighbors in their native communities, but highly toxic or inhibitory to native plants in introduced ecosystems (Muller, 1969; Callaway & Aschehoug, 2000; Bais *et al.*, 2003; Hierro & Callaway, 2003; Ahmed *et al.*, 2007).

Concept of invasibility and invasiveness

The term "invasibility" emerged in the field of invasion ecology to describe the susceptibility of an environment for invasion. In constitutes the vulnerability of the ecosystem to biological change (Milbau *et al.*, 2003). It is the susceptibility of an environment to the colonization, establishment, and proliferation of individuals of a species into introduced community (Davis *et al.*, 2005).

Invasiveness indicates those attributes or characters that make a species invasive (Lake & Leishman, 2004). Different traits for the success of invasive species are discussed: e.g. self fertility (Baker, 1965), phenotypic plasticity (Gray, 1986), intrinsic growth rates (Crawley, 1986), competitive ability (Byers, 2000), vegetative growth (Rejmanek, 2000), dispersal (Lake & Leishman, 2004), and genetic plasticity (Dawson *et al.*, 2009).

Invasion in the tropics

There are various investigations on invasibility related to temperate forests in the last two decades. But very few studies have been dealt with the invasibility of tropical forests (but see Drake *et al.*, 1989; Frayer, 1991; Walker & Vitousek, 1991; Turner & Tan, 1992; Fine, 2002; Biswas *et al.*, 2007). Tropical forests' invasibility is mostly investigated at the example of isolated tropical oceanic and continental islands and archipelagos. These are offering the experimental setting for precise observations (e.g. tropical Society Islands, Hawaii Island, tropical Indo-Pacific islands) (Loope & Mueller-Dombois, 1989; Vitousek & Walker, 1989; Walker & Vitousek, 1991; Meyer, 1996; Meyer & Florence, 1996; Conant *et al.*, 1997; Medeiros & Loope, 1997; Meyer, 1998; Fine, 2002; Denslow, 2003; Mack & D'Antonio, 2003; Allison & Vitousek, 2004; Meyer & Lavergne, 2004). However, insights gained in tropical ecosystems on islands, though important, are only in parts transferable to tropical forests on the mainland. Due to very specific characteristics (e.g unsaturated species pool; low competitive ability of natives; lack of invader-specific herbivores and pathogens), island ecosystems are said to be more invasible (Elton, 1958; Loope & Mueller-Dombois, 1989; Simberloff, 1997; Lonsdale, 1999; Simberloff & Von Holle, 1999; Mack *et al.*, 2000; Denslow, 2003; Dewalt *et al.*, 2004; Meyer & Lavergne, 2004; Fridley *et al.*, 2007). Moreover, the number of exotic plants on islands is increasing at an alarming rate with the development of commercial trade, the diversification of agriculture, tourism activities, and especially the practice of 'green industry' of ornamental plants (i.e. plant nurseries, gardening and horticulture activities) (Lonsdale, 1999; McNeely *et al*, 2001; Meyer & Lavergne, 2004). As a result, the total number of alien pant species that are introduced in tropical islands exceeds the number of indigenous species in many cases.

Tropical forests in general are said to be more resistant against invasion than other ecosystems because of their high diversity in terms of both species and functional groups (Elton, 1958; Fine, 2002; Inderjit *et al.*, 2005). Most tropical forests are dominated by vertebrate-dispersed plants, while most of the exotic herbaceous species are not vertebrate dispersed (Rejmanek & Richardson, 1996; Fine, 2002). Consequently, as long as vertebrate dispersal is not restricted in undisturbed tropical forests, there is little chance for the successful invasion of exotic plants. In addition, most plant invaders are not shade tolerant (Baker, 1974; Mack, 1996). However, different types of forests may respond to invasions in different ways. Extreme habitat conditions, which are the characteristics of most tropical ecosystems, make ecosystems less invasible even in case of disturbance (Lugo, 1999; Fine, 2002). Tropical ecosystems exhibit weathered and nutrient-poor acidic soil (Sanchez *et al.*, 1982). Especially the high resource turnover, nutrient poor soil, and competition for light enhance the resistance of tropical forests against invasion. Moreover, the understorey of undisturbed tropical forests receives little amount of light (1-2% of full sunlight) compared to temperate forests (3-4% full sunlight) (Canham *et al.*, 1990). This limitation of light may be a filter for many exotic species. However, fewer studies are available on invasion in tropical forests (Fine, 2002; Wright, 2005; Fridley *et al.*, 2007). In temperate regions especially in Europe, there is a specific time line for the introduction (e.g. the year 1492). However, it is very difficult to track the temporal history of non-native species introduction in the tropics.

However, tropical forests worldwide are under high human pressure due to land utilization and timber harvest (Phillips, 1997; Sala *et al.*, 2000; Bawa *et al.*, 2004; Wright, 2005). These anthropogenic disturbances act as an effective agent to increase the invasibility of tropical communities either simultaneously interacting with other disturbances (additively or synergistically) or separately. In general, studies from other zones found a positive correlation between invasibility and disturbances (D'Antonio & Vitousek, 1992; Knops *et al.*, 1995; Kotanen *et al.*, 1998; Mack & D'Antonio, 1998; Fine, 2002; Ross *et al.*, 2002; Gelbard & Belnap, 2003; Buckley *et al.*, 2003; Weber, 2003; Lockwood *et al.*, 2007). Highly disturbed (i.e. deforested or fragmented) tropical forests whether on mainland or island possess or facilitate the spread of exotic species (Fine, 2002). The invasibility of old-growth tropical forests will be surprisingly increased if these anthropogenic disturbances continued in the form of fragmentation and degradation (Wright, 2005).

Biodiversity in the tropics

Tropical forests are the global epicenters of biodiversity (Lewis, 2006) and are representing the largest terrestrial reservoir of biodiversity from the gene to the habitat level (Mayaux *et al.*, 2005). They are the most biologically diversified and ecologically complex ecosystem in the world (Laurance, 2007). This diversity of vegetation, ranging from species rich rain forest to denuded desert, that makes the tropics more diverse (Evans & Turnbull, 2004). Tropical forests support millions of people providing shelter (e.g. homes, building materials), subsistence (e.g. food, medicine), and cultural identity (Lewis, 2006).

Tropical forests cover less than 10% of the land surface in the world, but they accommodate between one-half and two-thirds of the world's species (Groombridge & Jenkins, 2003). They support more than 200,000 species of flowering plants, which include many tree species (Prance *et al.*, 2000). Tropical forests include a variety of ecosystems such as moist or rain forests, mangroves, montane forests, dry forests and wooded savanna systems (Lewis, 2006). According to country estimates from FAO (2001), there are 1803 million ha of tropical forests in 2000 of which 49% in America, 34% in Africa and 16% in Asia. Species composition varies dramatically between different systems.

Special vulnerability of tropical forests to invasion and biodiversity loss

Tropical forests and their biota are experiencing a number of threats (Phillips, 1997; Wright, 2005; Laurance & Peres, 2008), which might result in biodiversity loss and open the forest for invasive species (e.g. population pressure, land use change; climate change; deforestation and fragmentation; plantation etc). There are strong enforcing interactions among these threats that might accelerate both biodiversity loss and invasibility of tropical forests.

Population density is the greatest challenge for tropical forests. All anthropogenic activities that have an effect on tropical forests originated from the increasing population pressure (especially the rural population density) on these forests (Peres *et al.*, 2006). The population of tropical countries was 1.8 billion in 1950 and increased to 4.9 billion in 2000. A further increase by an addition of 2 billion before 2030 is expected (United Nations, 2004). Wright & Landau (2006) demonstrated a strong negative linear relationship between the human population density and the forest cover in the tropics. In many tropical regions, the fallow periods for shifting cultivation are often reduced or even eliminated due to the high population pressure and agricultural intensification (Parrotta *et al.*, 1997).

Rapid land use changes also have a strong negative impact on biodiversity in tropical forests followed by climate change, nitrogen deposition, biotic exchange or increased carbon dioxide concentration for terrestrial ecosystems (Sala *et al.*, 2000). Tropical forests of the world are degrading at an alarming rate because of high human disturbances like deforestation and fragmentation (Wright, 2005; Lewis, 2006; Wright & Landau, 2006; Laurance, 2007). The highest rate of clearing was found in Tropical Asia (0.62% per year) followed by Latin America. Paraguay, Indonesia and Madagascar have the highest clearing rates (Hansen & DeFries, 2004). Bangladesh is not an exception regarding increasing population density. Deforestation and fragmentation are responsible for the both biological invasion by exotic species and biodiversity loss in the tropics (Wright, 2005).

Hunting and poaching or defaunation is one of the other greater human induced challenges for tropical forests (Phillips, 1997). Human hunters defaunate and threaten many keystone species like primates and other large vertebrates throughout the tropical forests (Schwartzman *et al.*, 2000). The animals favored by the hunters are often the most important agents for seed dispersal as well as for the carnivorous predation that help to structure both plant and animal communities (Wright, 2005). This defaunation ultimately leads to decrease of native plant species richness in the tropics. Hunting is one of the major causes for the extinction of island birds (Duncan & Blackburn, 2007). Consequently, it decreases the native biodiversity and makes room for the invasion by alien species.

Only about 25% of *plantations* worldwide are located in the tropical and subtropical regions but the rate of expansion is increasing (Kanowski, 1997). The rate of plantation expansion in the tropical forests was reported by the FAO at 1.8 million ha per year (FAO, 1993). Due to deforestation, degradation, rural-urban migration (urbanization) etc. plantation as well as secondary forest succession play a vital role for the restoration of ecosystem health and productivity in the tropics. They have conservation value in tropical regions and accelerate recovery and restore productivity, biodiversity and the subsequent natural forest succession (Evan &

Turnbull, 2004). But the challenge for tropical forests is that alien plant species have been selected for rehabilitation and restoration. Thus, these plantation species are likely to impact the biodiversity of tropical forests. Moreover, exotic species introduced based on special characteristics bear a higher risk of becoming invasive. Some species of woody legumes introduced in tropical countries are already invading native ecosystems (Hughes & Styles, 1989).

There is evidence that *climate change* will dramatically affect tropical forests (Lewis, 2006). Especially, a shift in vegetation, which is very likely associated with a change in species composition due to differing dispersal abilities, might trigger invasion. Since the 1970s, tropical temperatures have increased by 0.26 ^{o}C (Malhi & Wright, 2004). There are numerous examples were a warming process has altered the geographic distribution of numerous native species (Kreyling *et al.*, 2010). Moreover, a change in precipitation, together with drought effects induced by climate change, affects recruitment, composition and diversity of tropical forests communities globally (Engelbrecht *et al.*, 2005; Engelbrecht *et al.*, 2007; Comita & Engelbrecht, 2009). These might encourage the invasibility of the ecosystem by influencing the resource availability. Since the 19th century atmospheric CO_2 concentrations have increased by 30% (Wright, 2005). An elevated CO_2 was reported to increase the long-term success of exotic species in ecosystems (Dukes, 2002).

Biodiversity and invasion in Bangladesh forest ecosystems

Bangladesh is located in the north-eastern part of South Asia with an area of 14.8 million ha. (Ahmed, 2008). It lies between 20^{o}34$^{'}$ and 26^{o}38$^{'}$ northern latitude and 88^{o}10$^{'}$ and 92^{o}41$^{'}$ eastern longitude. It has monsoonal tropical to subtropical climate. Mean annual rainfall varies between from 1500mm in the north-west to more than 5500mm in the north-east (Das & Alam, 2001). Most precipitation occurs between the end of May and August. The average minimum temperatures lie around 10^{o}C and the maximum summer temperatures range from 32^{o}C to 35^{o}C. High humidity is reported during the monsoon, which is more than 80 percent (Das & Alam, 2001). Most of the country is formed by the Ganges-Brahmaputra-Meghna (GBM) delta, while hilly areas lie along the eastern parts of the country (Rashid, 2008) (Figure 1).

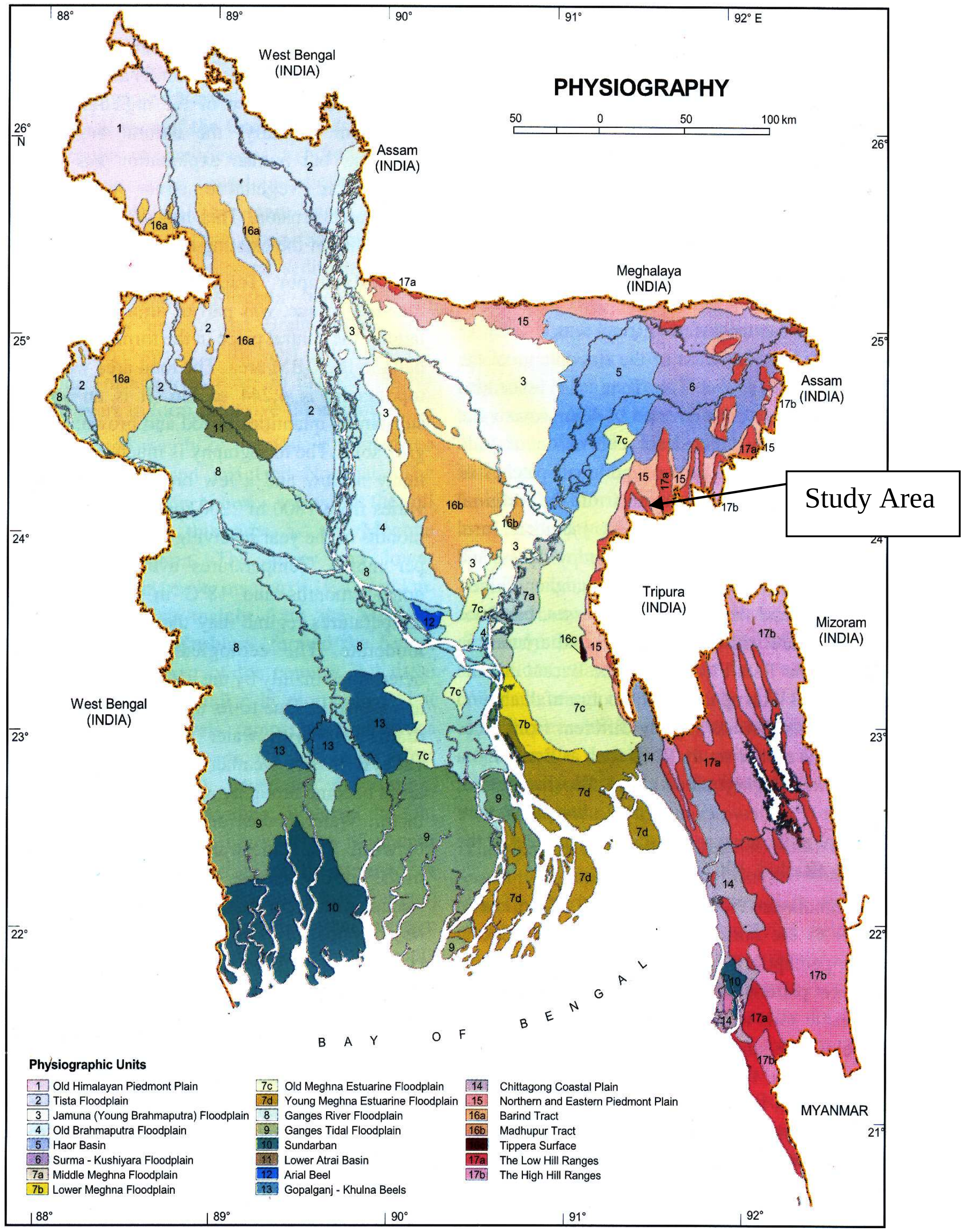

Figure 1. Physiography of Bangladesh. *Source:* Rashid (2008).

Bangladesh has a total of 2.53 million ha of forestedland (i.e 17.1% of the total area). However, only 0.84 million ha (5.7%) is in under dense tree cover. The forest area is mainly distributed in the eastern and south-eastern hills, central terraces and in the south-western mangroves (Alam, 2008) (Figure 2).

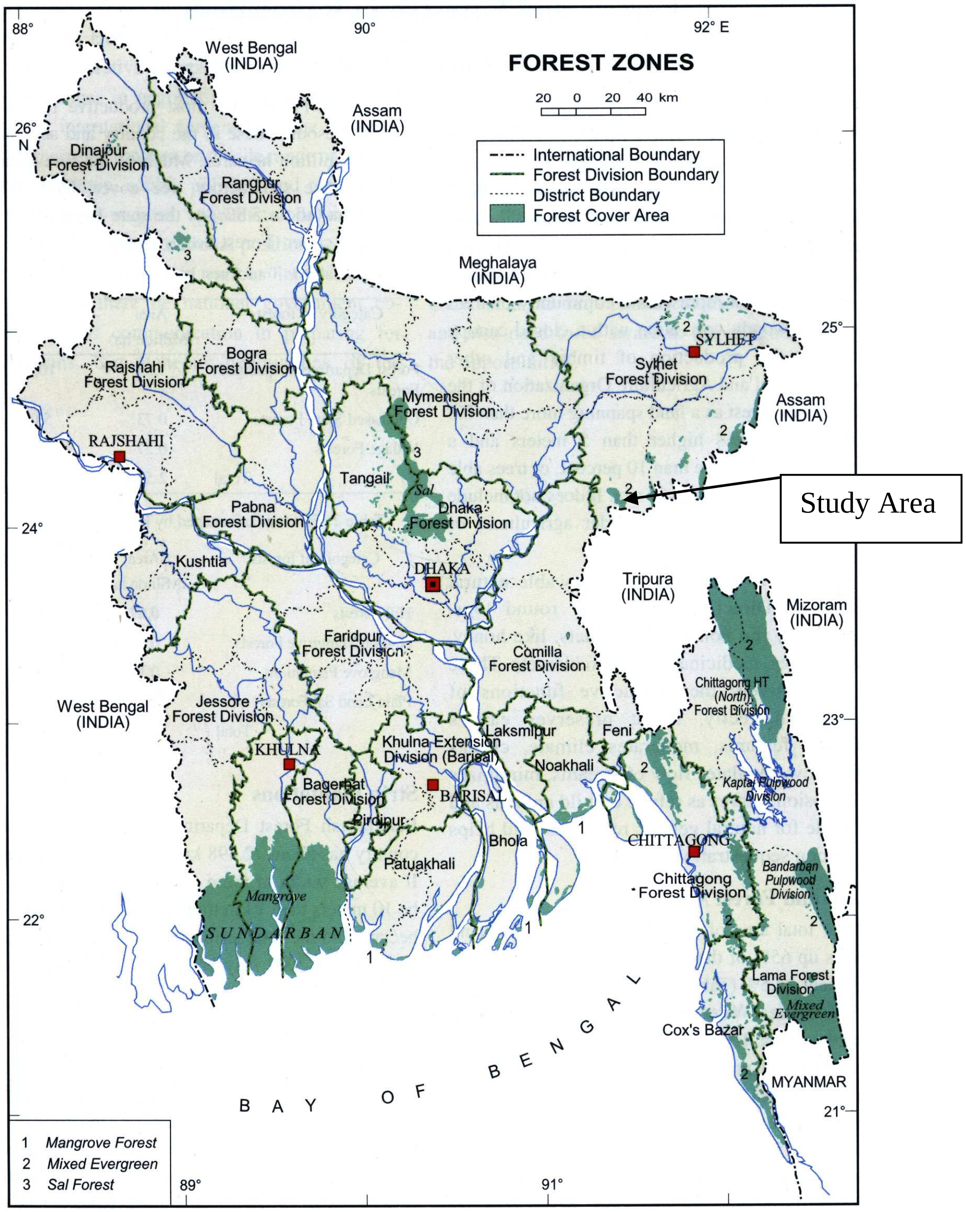

Figure 2. Forest areas of Bangladesh. *Source:* Alam (2008).

Hill forests contain the evergreen and semi-evergreen vegetations. They are mainly situated in the greater districts of Chittagong, Sylhet, and the Chittagong Hill Tracts (CHT). Hill forests support rich genetic reserves. However, during the last few decades hill forests have been reduced and degraded mainly due to agricultural land clearing, shifting cultivation, encroachment, over-exploitation etc. Bangladesh is a highly populated country where increasing population pressures render tremendous pressure on its natural resources in the forests. The creation of protected areas is a key strategy to counteract the biodiversity loss in the tropics (Heywood, 1995). At present, most of the natural forests are being managed through the declaration of protected areas, as protected areas are considered to be the most scientific way of conservation of ecosystem, species and genetic resources. There are 24 protected areas in Bangladesh, which have been declared by the Forest Department in both terrestrial and aquatic ecosystems. In most cases, they possess distinctive ecosystem and support a high number of genetic resources (Khan *et al*., 2008).

Plant introduction is a traditional practice. Over a long period of time, plants of various types of economic importance have been introduced in Bangladesh. It is said that the first introduction was made by British people through alien water hyacinth (*Eichhornia crassipes*) from Brazil as its decorative flowers were adored by British ladies (Islam *et al*., 2003). In Bangladesh, most of the exotic species were introduced by British people in 19th century from different countries or geographic areas of the world. Altogether more than 300 exotic species have been introduced up to date. Herbaceous and lianas are the dominant groups followed by trees and shrubs (Hossain & Pasha, 2001). However, it was not possible to find a complete list of introduced alien species for Bangladesh. It is estimated that more than one hundred alien species that have been introduced to Bangladesh are difficult to identify as exotic as they are already naturalized and growing like native species (Hossain & Pasha, 2001).

Some of introduced species have impact on native diversity. They suppress the growth of native species through their luxuriant growth (Hossain & Pasha, 2001). Moreover, their slowly degradable leaves pose a threat to the native flora and fauna. Additionally, they use local resources such as soil moisture and nutrients. This ultimately may reduce soil fertility (Barua *et al*., 2001). As their fruits are not edible, they do not accommodate wildlife. Moreover, the pollen grains of these trees create allergy in the respiratory tracts of human beings. The threat posed to natural habitats by these alien invasive plants is becoming a major concern among the conservationists, ecologists, foresters, policy makers and scientists in Bangladesh.

However, up to date no study has been conducted regarding the patterns of biological invasions and the influence of habitat characteristics and nature conservation on biodiversity patterns in hill forests ecosystems of Bangladesh. Due to the lack of previous studies, this dissertation makes a first attempt for this ecosystem.

Objectives, Research Questions and Hypotheses

The overall motivation of this thesis can be concentrated into two main issues: (1) exploring the biological invasion in the tropics including knowledge on invaders, patterns, mechanisms, drivers, effects, vulnerability of ecosystem, research gaps and (2) identifying the patterns of biodiversity and stand characteristics in an anthropogenic landscape and the influence of conservation patterns on biodiversity in the study area. Considering the first issue, a formalized literature search in the ISI Web of Science (Thomson Reuters) was made to see whether biological invasion in the tropics is comparable to other climatic regions. Subsequently, a case study was done in the tropical forest ecosystem in Bangladesh to deepen the understanding of exotic species. Finally, the number and percentage of exotic species were modeled to predict the relationship with native species richness as well as with other environmental and disturbance variables. The later focuses on the landscape patterns of biodiversity and stand characteristics in the study area and the factors explaining these patterns.

Biological invasion has attracted considerable attention for its adverse effects on biodiversity (Mack *et al.*, 2000). Most of the invasion studies were done in temperate and other regions (e.g. Burke & Grime, 1996; Prieur-Richard *et al.*, 2000; Dukes, 2001; Hector *et al.*, 2001). Tropical forests are the global epicenters of biodiversity (Lewis, 2006). Biological invasions are also affecting the functioning of earth's most diverse ecosystems (Phillips, 1997). However, very few studies were conducted on invasive species as well as patterns of species invasion in tropical forests, specifically the continental old-growth tropical forests (Drake *et al.*, 1989; Frayer, 1991; Walker & Vitousek, 1991; Turner & Tan, 1992; Fine, 2002; Wright, 2005; Fridley *et al.*, 2007). Besides, tropical invasibility has mostly been studied on islands ecosystems rather than mainland forests (Mack & D'Antonio, 2003; Allison & Vitousek, 2004; Meyer & Lavergne, 2004). These island invasions perhaps can not be considered as representative for tropical invasions. Thus, a high importance of review becomes clear addressing the extent of invasion study on in the tropics as well as the patterns, drivers, mechanisms, effects, and finally to realize the gaps in current knowledge of invasions in the tropics. We emphasized certain questions in this regard: Are invasion patterns in the tropical forests comparable to other climatic regions or are they a special, distinctive case? What are the effects, drivers, mechanisms and forest types mostly discussed in the tropical forest invasions? Where are the gaps in current knowledge of invasions in tropical forests **(Manuscript 1)**?

After conducting this review, I was very much interested to make a case study observing the patterns of invasions and the biotic features of invaders in a Bangladesh forest ecosystem **(Manuscript 2)**. For understanding the biological invasion, it is very critical to know the underlying processes that facilitate the success of exotic species (Hill et al., 2005) as well as the attributes of the invasive species regarding the taxonomic position, biogeographic and climatic origin, and life-forms (see also Pyšek, 1998).

Various hypotheses and theories have been proposed to explain the susceptibility of communities to invasion. One of the earliest theories from Elton (1958) argued that diverse communities should be more resistant to invasion than species-poor ones. Changes in the availability of resources such as light, water and nutrients can increase the susceptibility of a community to invasion (Lake & Leishman, 2004).

A general theory on community invasibility by Davis *et al.*, (2000) states that “a plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources” i.e. invasibility is proposed to be positively correlated with resource availability. It is another general, very common and historical idea in ecological theory, that disturbances offer favorable conditions for the establishment of invasive species through the alteration of resources in ecosystems (Knops *et al.*, 1995; Kotanen *et al.*, 1998; Fine *et al.*, 2002).

Though there is a growing consensus among ecologists and environmental biologists to investigate the underlying processes related to invasibility as well as the ecological and biogeographical attributes related to invasiveness, however, very few researches have been conducted in Bangladesh forest ecosystems where invasion has been influenced by migration and dispersal for thousands of years. Most of the studies were in the form of simple enumerations such as, listing names, sources of origin and occasionally possible effects (e.g. Barua *et al.*, 2001; Hossain & Pasha, 2001; Islam *et* *al.*, 2003; Akter & Zuberi, 2009). I did not find any literature which explicitly addressed the biotic features; drivers e.g. disturbances; environmental variables and the effect of native species richness on invasion patterns (but see Biswas *et al.*, 2007).

The aims of **Manuscript 2** were to get an insight into introduced species in tropical forest ecosystems of Bangladesh and to analyze the spatial distribution of exotic species with respect to disturbances, environmental variables, and native species richness. Specifically, the following proposed hypotheses were formulated: 1) Exotic species richness decreases as native species richness increases in the study area; 2) Exotic species richness increases with increased availability of resources such as soil and environmental resources; 3) Exotic species richness increases with the proximity and intensity of disturbances.

The relationships among habitat characteristics, conservation, and plant diversity are important parameters to predict biodiversity patterns in tropical forests (Engelbrecht *et al.*, 2005; Hernandez-Stefanoni, 2006; Comita & Engelbrecht, 2009). Generally, species abundance and composition are noticeably influenced by the environmental differences between landscapes. Since disturbance is one of the most functional elements of landscape, it is also one of the most prominent factors in controlling the biological diversity (Roberts & Gilliam, 1995). Tropical biodiversity is mostly threatened by anthropogenic disturbances mainly through land use or land cover change (Sala *et al.*, 2000). Forest biodiversity of Bangladesh is not an exception. There, biodiversity is threatened due to land use changes caused by one of the highest human population densities on earth (1099.3 people per km^2).

Many studies have been done to describe the species richness patterns. However, less information is available for stand characteristics and the beta diversity patterns i.e. how species composition varies in space and how heterogeneous ecosystems are (Duivenvoorden *et al.*, 2002). Specifically, few attempts have been made in order to explore precisely the spatial patterns of biodiversity (both alpha- and beta-diversity) in tropical forest ecosystems of Bangladesh. The purpose of **Manuscript 3** was to address these issues. Here, it was questioned how species richness patterns (alpha-diversity) and spatial heterogeneity (beta-diversity) is related to measurable environmental conditions, disturbance regime, and nature protection? It is hypothesized that nature protection has positive effects on both alpha and beta diversity.

The stand characteristics and spatial species turnover or beta-diversity was in the focus of Manuscript **4.** It provides first insights into the decay of floristic similarity over distance and stand characteristics. The later has an important role in forest management and planning as it indicates the productivity of forest ecosystems (Köhl, 1993; Chhetri & Fowler, 1996). Here, I used tree species in a tropical forest ecosystem in Bangladesh as an example for spatial trends in similarity. The similarity between two observations usually decreases or decays as the geographic distance between them increases. This general finding is also called the first law of geography (Tobler, 1970). This distance-decay relationship has proven to be an effective way to analyze how the similarity in species composition between two communities varies with the geographic distance between them (Nikola & White, 1999; Condit *et al.*, 2002; Soininen *et al.*, 2007). The purposes of our study were: 1) to characterize and examine the stand characteristics in the study area; 2) to investigate the pattern of tree species similarity as a function of geographical distances; 3) to analyze that how much variation was explained by geographical distances.

Synopsis

Thesis Outline

This thesis comprised of four manuscripts. These are arranged according to two main issues that are dealt with in the thesis. The first issue is on the knowledge of biological invasions in the tropics and distribution of exotic species with respect to the underlying processes and taxonomic disposition **(Manuscripts 1 & 2)**. The second issue focuses on the landscape patterns of biodiversity with respect to the factors that shape these patterns **(Manuscripts 3 & 4)** and the stand characteristics of forests. A brief description of each of the manuscripts is provided in the subsequent paragraphs.

Manuscript 1 highlights the problem and screens the knowledge of biological invasions in the tropical forests. It deals with the effects, drivers, mechanisms of invasions discussed in tropical forest ecosystems as well as the gaps of knowledge with respect to biological invasions in the tropics. A formalized literature search in the

ISI Web of Science (Thomson Reuters) was carried out. In general, the biological invasion researches in tropical forests are underrepresented. Though, few studies have been affected on animals, mainly invertebrates. However, here, we focus on biological invasion by plants. Within our formalized literature search, it was revealed that most of the invasion studies carried out in the tropical forests concentrated on the effects of invasion on ecosystem structure rather than ecosystem processes/function. Most of the studies analyzed the effect of invasion on species richness, reproduction and recruitment. Then we had a closer look on the drivers of invasions in the tropical forests both for the ecosystem's invasibility and invader's invasiveness. Most of the studies covered by our formalized literature search indicated that disturbances: anthropogenic and natural, and availability of more resources i.e. empty niches, are the major drivers for ecosystem's invasibility. On the other hand, ecological amplitude and high dispersal rates are mostly responsible traits for the invasiveness of exotic species introduced in tropical forests. Most of the studies in tropical forests supported the disturbance hypothesis and the empty niche hypothesis. Considering the biogeographic aspects, the majority of the studies were conducted in continental as well as oceanic islands or archipelagoes. With respect to the forest types, the majority of the studies have been conducted in evergreen tropical rainforests. Based on this literature study, gaps in current knowledge of biological invasion in the tropical forests are discussed. Researches in different mainland/continental tropical forests other than evergreen tropical rainforests are urgently needed.

Manuscript 2 gives an insight into exotic species as well as the patterns of invasion by alien species in Bangladesh forest ecosystems. The biotic features of exotic species were explored using the information from Encyclopedia of Flora and Fauna of Bangladesh and by using comparisons available in other studies. Boosted regression trees (BRTs) and Detrended correspondence analysis (DCA) were applied i) to assess the relationship of explanatory variables viz. native species richness, environmental variables and disturbances with the number and the percentage of exotic species; ii) to visualize the distribution of exotic species with respect to these explanatory variables. Our results suggested that a high proportion of exotic species were introduced mainly with the purposes of timber and fuel wood production from the other tropical regions of the world. Most of the exotics are trees. Majority of the plants belong to the families *Fabaceae*, *Asteraceae*, *Malvaceae*, and *Verbenaceae*. Native species richness has been found as the best predictor for exotic species richness and percentage through predictive modelling based on boosted regression tree analyses. However, there are considerable differences with respect to the relationships between native and exotic species richness in different protection status. Environmental variables revealed less explanatory power. However, exotic species richness and percentage increases with increasing phosphorus, number of disturbances and bulk density while the same decrease with increasing elevation. Considering the distribution, based on ordination by DCA, surrounding areas accommodate more exotic species as they are associated with more number of disturbances. Our results suggest that disturbances, both anthropogenic and natural, support the establishment of exotic species in this tropical forest ecosystem.

Manuscript 3 deals with the spatially explicit analysis of drivers and patterns of biodiversity in Bangladesh forest ecosystems. It provides a special focus on plant species richness and heterogeneity patterns with respect to soil properties, topographic conditions, disturbance regime, and conservation patterns. Multivariate approaches, similarity analyses using Sørensen Index and variation partitioning were applied to predict the drivers and patterns of biodiversity along environmental, disturbance and protection gradients. The results revealed that plant species richness and species composition is strongly related to a disturbance gradient. They are also strongly correlated with environmental variables and protection in colinearity with the disturbance regime, while the environmental variables were mainly explained by elevation. Major effects of soil conditions mainly soil moisture were observed on species composition rather than species richness. The influence of disturbances on species composition is less than on the species richness pattern. Probably as a result from that, similarity in species composition in reserve forest is lower than that of national park and surrounding areas. However, most of the explained variation was explained in colinearity with the disturbance regime while little variation was explained independently from the disturbance regime. Protection is the second important predictor. Thus, the strong colinearity of biodiversity patterns with the disturbance regime and protection has important conservation implications. It indicates the effectiveness of protected areas to conserve the nature and natural resources in Bangladesh forest ecosystems as well as in the tropics.

Manuscript 4 deals with the stand characteristics and one of the most widely applied relationships in ecology and biogeography, which explain spatial biodiversity patterns through species turnover along spatial environmental gradients with distance. We measured diameter at breast height (DBH) of each tree in our circular plot to determine the stand characteristics in this forest ecosystem. Then we assessed the distance-decay relationship using tree species frequency in a tropical forest ecosystem of Bangladesh. It provides insight into the pattern of spatial species turnover. Bray-Curtis index of similarity was calculated as it takes consideration of the quantitative information of every single species. Our findings suggested that biomass increases significantly with protection status while the trees in the surrounding areas were more vigorous. This may be mainly due to the well-managed shade trees in the surrounding tea gardens of economic interests. The results revealed a general distance-decay pattern i.e. similarity in species composition was negatively correlated with geographical distance. However, the slope of the decay was much steeper in the Reserve Forest than in the National Park. As the Reserve Forest has a less uniform habitat in comparison with the National Park, habitat diversity might be a good explanation for the larger spatial species turnover in the less protected area. Nevertheless, the geographical distance still could not explain the major portion of variation of floristic similarity. Thus, also other drivers of dissimilarity such as land use practise, environmental heterogeneity have to be considered (and maintained).

Synthesis and Conclusions

Invasions in the tropics: It is documented that biological invasions by introduced species pose a serious threat to the biodiversity of natural communities world-wide. Invasion has been reported for its adverse effect on ecosystem structure and function (Cronk & Fuller, 1995). Research on invasion ecology has remarkably increased over the last few decades. Still yet, it’s a major challenge for ecologist to understand the two important terms in biological invasion viz. invasiveness of species and invasibility of habitats. This dissertation contributes to the development of strategies and solutions for this challenge.

Biological invasions are important drivers of vegetation and ecosystem functioning in tropical ecosystems, as well as in other ecosystems. It is well-established knowledge that tropical forests are currently losing biodiversity. One of the major causes for this trend is the invasion by alien species. However, invasion studies in tropical forests are scarce. Moreover, there is lack of new ideas that stimulate as well as implicate future invasion research in tropical forests.

The **Manuscript 1** discusses the gaps in current knowledge in invasion ecology in the tropics based on a formalized literature survey. A general trend of research was observed like temperate and other zones. Overall, reported effects, drivers, mechanisms of plant invasion in the tropics do not differ strongly from other biomes. However, still fundamental questions remain unexplained and are posing challenges to research. This review provides an encouragement for future studies on invasion ecology in the tropics. Considering the effects of invasion, future studies on ecosystems processes are highly recommended. Moreover, the mechanisms/processes underlying the effects of exotic plants invasions are poorly understood. Therefore, the exploration of these pathways or mechanisms (e.g. allelopathy, N-fixation, genetic modification) is appreciated for future research. The unbalanced proportion of studies in different types of tropical forests suggests to consider other tropical forests than tropical evergreen rainforest for future research.

Exotic species invasions in the tropics with respect to native species richness, environmental variables and disturbances: It is essential to answer some critical questions in invasion research to get a better insight into invasion. What is the role of native species richness, environmental variables including disturbances in determining the success of exotic plants in tropical forests? The results of **Manuscript 2** attempted to determine these biotic features and to examine whether particular environmental variables or disturbance are facilitating the success of exotic species in a tropical forest ecosystem. Most of the exotic tree species in this case study were introduced during the 19th and 20th century mainly for the development of forestry (Islam *et al.*, 2003). A major portion of exotic species in the study area are originated from other tropical ecosystems in the world (Stadler *et al.*, 2000). The largest families of flowering plants (e.g. *Fabaceae*, *Asteraceae*) contribute to the major portion of exotic species in the study area. Although our analyses are providing insights into certain important functional attributes of exotic invaders in the study area, it is recommended that future studies should investigate more in detail the ecological and physiological characters of successful invaders.

It has been hypothesized that high species richness increases the resistance of a community to invasion. Field observations are supporting that hypothesis (Elton, 1958; Fox & Fox, 1986). However, this field of research is filled with contradictory results and assumptions with respect to different protection status. Our field study supported the mentioned hypothesis, assuming that the number and the proportion of alien species are responding negatively to the increasing native species richness in surrounding areas. However, in case of reserve forest the relationship is unimodal and hump-shaped. More future research over broad spatial gradients is recommended to explore this phenomenon.

Attempts have been made to identify “invasibility” characteristics. The susceptibility of the study area for the establishment of exotic species is associated with resource availability and disturbances. However, the boosted regression trees analysis revealed, that both variables explain only little amount of variation. The results further on indicated that highly elevated and relatively undisturbed protected areas are less susceptible to invasion by exotic species. However, other characteristics such as site history, propagule pressure are more important for future study in determining exotic species success in the study area.

Landscape patterns of biodiversity, stand characteristics and conservation implications: The findings of **Manuscripts 3 and 4** contribute to the explanation of the stand characteristics of forests; and the drivers, patterns and conservation implications of biodiversity loss in the tropics - specifically in the case study area in Bangladesh. Stand characteristics have high implications for forest management and planning. The biodiversity in the tropics are facing an array of threats induced from different scale of anthropogenic disturbances (Peres *et al.*, 2006). This is why, tropical biodiversity is strongly influenced by habitat characteristics and conservation patterns (Engelbrecht *et al.*, 2005; Hernandez-Stefanoni, 2006; Comita & Engelbrecht, 2009). Tropical forest landscapes are changing rapidly. One driver is the global economy and international companies. The other one is more prominent, here. As the population of tropical countries increase, the pressure on forest ecosystems and land surface increases too. This is regarded to be one of the greatest challenges for tropical biodiversity conservation (Wright, 2005). Bangladesh is one of the most populated countries in the world. It is hosting 1099.3 people per km^2. During the last centuries and increasingly the last decades, the forests of Bangladesh have been destroyed by degradation and land use changes, first of all to meet the increasing human needs. Bangladesh has only about 5.7% forested land with dense tree cover. However, it has 17.1% of forestland in its land surface (Alam, 2008). An estimated 5700 species of angiosperms alone are available in the forests of Bangladesh (including 68 woody legumes, 130 fiber yielding plants, 500 medicinal plants, 29 orchids) of which some 2259 species are reported from the Chittagong hilly regions (Khan *et al.*, 2008). However, anthropogenic influences are posing negative impacts on this biodiversity and stand characteristics. Consequently, as a tropical country, Bangladesh support very few remnants of long term established ecosystems.

Manuscript 3 depicts a clear picture about the patterns of biodiversity in a Bangladesh forest ecosystem considering all these issues. We found that biodiversity patterns are positively correlated with protection and elevation while negatively with disturbances. Finally, the results of this manuscript demand more extensive studies of the protection of species richness and composition from the expected future human impacts. Moreover, more researche is needed to develop a framework for biodiversity conservation as an integrated forest area management, where one of the primary goals will be the sustainable use of forest biodiversity. Additionally, remote sensing applications are strongly recommended from our findings, which might allow rapid assessment for future comparisons.

Finaly, we made an effort to examine and characterize the stand characteristics as well as to describe a methodological approach for spatial patterns of species turnover in the study area **(Manuscript 4)**. In this study, we calculated DBH as a measure of biomass and stand characteristics and investigated the pattern of floristic similarity as a function of geographical distances between plots of the study area. Our studies identified management as an important option to maintain stand characteristics. Moreover, it is well documented that alpha-diversity is intensively studied in various tropical forests. However, studies on beta-diversity or species turnover, which is controlling the diversity in ecological communities, are underrepresented (Condit *et* *al.*, 2002; Duivenvoorden *et al.*, 2002; Baselga, 2007; Jurasinski *et al.*, 2009; Desalegn & Beierkuhnlein, 2010; Tuomisto, 2010a; Tuomisto, 2010b). Our findings recommend future studies to identify the major determinants of these characteristics and the spatial species turnover in more communities at different scales as they have high implications for biodiversity conservation.

At a glance the following research gaps were identified for future research from my thesis:

1. Invasion research in the tropics is underrepresented in comparison to temperate regions. The effects, drivers and mechanisms of invasions should be intensively explored in different tropical ecosystems. The two most important attributes like ‘invasiveness’ of alien species related to their life-history characters and ‘invasibility’ of habitats or ecosystems related to their abiotic and biotic characters need to be investigated in more detail in tropical forests.

2. The stand characteristics, landscape patterns of biodiversity and the factors explaining these patterns are poorly understood in the tropics in general but particular in anthropogenic landscapes like Bangladesh. Understanding the patterns and mitigating the influences in the face of uncertain global change is one of the great challenges for ecologists, biogeographers and conservationists.

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List of Manuscripts and Specification of Own Contribution

Manuscript 1

Authors: Mohammad Belal Uddin, Juergen Kreyling, Manuel J. Steinbauer & Carl Beierkuhnlein

Title: **Neglected or Negligible? Biological Invasions in Tropical Forests**

Status: in preparation

Journal: Biological Invasions

Contributions: This is one systematic review based on formalized literature search in the ISI Web of Science (Thomson Reuters). I have searched all the literatures based on certain search strings. I have read completely all the relevant literatures. I have input and processed the data. I have analyzed the data obtained from the search. Then I have written the whole manuscript. I have made the actual formulation of sentences and paragraphs. Juergen Krelying has given me the instructions for this search. Then he reviewed the manuscript. Manuel J. Steinbauer helped me to make the figures. Carl Beierkuhnlein has made critical review and final editing on the whole manuscript.

Manuscript 2

Authors: Mohammad Belal Uddin, Manuel J. Steinbauer, Anke Jentsch & Carl Beierkuhnlein

Title: **Exotic Plant Species in Bangladesh Forest Ecosystems**

Status: resubmitted after major revision (ID-BINV-2690 R1)

Journal: Biological Invasions (02/05/2011)

Contributions: This is one data based article. I have collected all the data from Bangladesh forest ecosystem through my intensive field work in Bangladesh. I have input and processed the data. I have analyzed my data. Then I have written the whole manuscript. I have made the actual formulation of sentences and paragraphs. Manuel J. Steinbauer has helped me to analyze my data as well as to review the manuscript. Anke Jentsch has given me the instruction for the disturbance data collection as well as for analyses. Then she reviewed the whole manuscript. Carl Beierkuhnlein has made critical review and final editing on the whole manuscript.

Manuscript 3

Authors: Mohammad Belal Uddin, Manuel J. Steinbauer, Anke Jentsch & Carl Beierkuhnlein

Title: **The Influence of Habitat Characteristics and Nature Conservation on Biodiversity in a Bangladesh Forest Ecosystem**

Status: resubmitted after adapting the reviewer comments (ID-BITR-11-093)

Journal: Biotropica (19/03/2011)

Contributions: This is one data based article. I have collected all the data from Bangladesh forest ecosystem through my intensive field work in Bangladesh. I analyzed my data with the help of Manuel J. Steinbauer. Then I have written the whole manuscript. I have made the actual formulation of sentences and paragraphs. Manuel J. Steinbauer has also helped me to structure the manuscript. Anke Jentsch has given me the instruction for the disturbance data collection as well as for analyses. Then she reviewed the whole manuscript. Carl Beierkuhnlein has made critical review and final editing on the whole manuscript.

Manuscript 4

Authors: Mohammad Belal Uddin, Manuel J. Steinbauer & Carl Beierkuhnlein

Title: **Stand Characteristics and Spatial Species Aggregation in a Bangladesh Forest Ecosystem**

Status: submitted (ID-diversity-8690)

Journal: Diversity (02/05/2011)

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Biological Invasions, in preparation

Neglected or Negligible? Biological Invasions in Tropical Forests

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Abstract

In the face of rapid global changes, improved understanding of the processes and effects of biological invasion is urgently needed. Especially the highly diverse tropical forests are underrepresented in ecological research on invasions. A formalized literature search in the ISI Web of Science (Thomson Reuters) was conducted regarding invasion in the tropical and subtropical forests. Here we reviewed those 55 articles which focus on invasion related to plant species in tropical forests.

Ecosystem or community structure of tropical forest is altered by biological invasions. Most of the studies supported the two leading hypotheses for the success of invasion; the disturbance hypothesis, and the empty niche hypothesis. In general the successful invaders have the basic traits of broad environmental tolerances and high dispersability in tropical forests. However, the importance of physical disturbance and allelopathy by the invasive species appear to be unique pattern in tropical forests. Research on invasion of tropical ecosystems is biased by a large number of studies on islands and wet tropical forests. Thus research is especially needed in mainland and other tropical forests.

Key words: rain forest, biodiversity loss, invasibility, invasiveness, climate change

Introduction

Biological invasions are recognized as a serious threat to biodiversity (Lonsdale 1999; Mack et al. 2000; Seabloom et al. 2006). As a consequence, biological invasion are a priority issue in nature conservation. However, most knowledge about invasion processes is available for those areas of the world that are monitored since decades, which is not necessarily the same as the hot spots of biodiversity.

In addition, for the understanding of non-native or alien species, native species pools have to be known, which requires precise historical records for species distributions, which is rarely found in the tropics. As a matter of fact, non-native species are not necessarily invasive but may coexist for a long time period with native species after being established either by purpose or not by humans. In temperate regions and especially in Europe, certain dates are fixed for separating phases of introduction (e.g. the year 1492). However, such distinct temporal lines are hard to be defined for tropical areas, where human activity, migration and trade are ongoing processes that are reaching back even before the last glaciation period. There, it is difficult even to identify species that are definitively not influenced in their distribution by human beings. And finally, the categories and terms that are applied for invasion processes such as “exotic” species are also difficult and can be misleading in a tropical context. May be these problems in categorizing invasions and invasive species in the tropics are one reason for the small amount of research approaches. This is in a strong discrepancy with the current loss of biodiversity that is mainly going on in the tropics and that is related to a large part also to invasion processes.

Invasive species are non-native species that are performing a strong impact in the recently occupied region. They can disrupt properties, structure, function, and dynamics of entire ecosystems (Mack et al. 2000). Biological invasions thereby affect economic growth and food security (Naylor 2002). Negative impacts of invasions are not limited to natural systems, but are also threatening secondary forests throughout the world (Fine 2002; Lugo and Helmer 2004). Biological invasions may interact with other components of global change and speed up it. For example, invaders respond positively to the increased atmospheric CO_2 (Dukes and Mooney 1999; Dukes 2002). This prevalence of invaders on elevated CO_2 impacts ecosystems which ultimately causes global change (Lewis 2006). Climate change and biological invasions are considered as the most important ecological issues in the near future (Ward and Masters 2007). However, there are hints that the effects of climate change and biodiversity loss on invasibility of plant communities are additive without signs of interactive amplifications.

Tropical forests cover approximately 10% of the terrestrial continents, yet, they harbor between one-half and two-thirds of the species in the world (Lewis 2006). A large number of not yet found species ("unknown diversity") as well as a high variability within taxa ("hidden diversity") emphasize the value of these unique ecosystems. Yet, tropical forests include a very diverse array of forests differing considerably in abiotic circumstances and disturbance regimes (e.g. tropical moist or rain forests, dry forests, montane forests, savanna forest, mangrove forests etc.) (Lewis 2006).

While in general the understanding of biological invasion has been ever increasing in the last years (Gurevitch et al. 2011), knowledge about biological invasions in the tropics is scarce. Out of 4883 studies obtained for all years up to November 2010 in the ISI Web of Science with the search string: Topic=(invasion or invasive or "exotic species" or "non-native species" or invader*), 539 studies deal with the tropics broadly, and only 273 studies were conducted in the forests.

Patterns of biological invasions in tropical forests differ from other biomes. First, ecosystems have evolved over very long time, presumably causing saturation in number of species unrivaled by other biomes. Second, competition for light is considered to be the main selective pressure in most of the tropical forests and native species are highly specialized in this regard, thereby leaving few options for non-native species. On the other hand, extremely high numbers of species are available within formerly demarcated biogeographical realms (e.g. continents, islands). Biological exchange may therefore lead to a homogenization, and, thus, to a much stronger loss in biodiversity than in the well studied circum-polar biomes of the extra-tropical northern hemisphere.

Here, we review the knowledge about the effects of biological invasions in tropical forest ecosystems. In addition, we are categorizing the drivers of tropical invasions based on the invasibility of the ecosystems and invasiveness of invaders. We ask whether classic hypotheses for biological invasions also apply to tropical forests. Finally, we identify those tropical regions with high priority for future research.

Formalized literature search

A formalized literature search was conducted in the ISI Web of Science (Thomson Reuters) with the search string: Topic= ((invasion or invasive or "exotic species" or "non-native species" or invader*) and forest* and (tropic* or subtrop*)); timespan = all years; database = SCI-expanded; refined by: subject areas = ecology and document type = article in November 2010. The search yielded 273 articles. Within these 273 articles, 100 articles fulfilled the condition that they strictly focused on biological invasions. Here, we focused on studies stemming from tropical forests, i.e. located in zonobiomes I and II according to Breckle (2002). 55 of these primary research papers focused on invasions by plants in tropical forests while 25 studies have been conducted on animals, mainly invertebrates (19). Therefore, we focus on biological invasions by plants here.

Effects of biological invasions on ecosystem properties

The breakdown of biogeographic barriers is altering ecosystem structure and function globally (Liebhold et al. 1995; Lövei 1997; Dukes and Mooney 1999; Lonsdale 1999; Naylor 2002). Within our formalized literature search, declining native species richness is reported most frequently (65% of all articles), while alterations of the quantitative species compositions, which is a precondition for species loss, is studied less often (Figure 1). This corresponds well to previous reviews that are not restricted to the tropics (Meiners et al. 2001; Yurkonis et al. 2005).

Invaders are assumed to affect ecosystem processes in the tropics mainly due to shifts in community composition (Parker et al. 1999). Displacement of native species appears to be facilitated by a negative impact of invasions on recruitment and reproduction of native species (38% and 40%, respectively). Seed germination as well as seedling establishment of natives can be negatively altered (i.e. reduced or even non-existent) below the canopy of invaders (Walker and Vitousek 1991). Reproduction can be affected by the disruption of plant-insect relationships, i.e. decreased pollinator activity and pollination success (Ghazoul 2004).

Though, even positive effects of invasion on recruitment and growth of native species is reported by one study (Fischer et al. 2009). *Cinchona pubescens and Cinchona calisaya*, which has been recognized as the worst invaders globally (ISSG 2006), facilitates the regeneration and growth of native species in the Hawaiian archipelago. There are significantly more species and a higher proportion of endemic species in *Cinchona* invaded plots.

As a consequence of maladaptation to the use of resources from invasive species by decomposers and herbivores, invaders tend to produce significant amounts of litter. This can suppress the regeneration of native species (Barua et al. 2001; Islam et al. 2003). The accumulation of litter may also be an effect of special traits of invaders whose success can be supported by allelopathic compounds in some cases (Walker and Vitousek 1991). In addition to potential suppression of regeneration, altered litter quantity and litter quality slows down litter decomposition and nutrient cycling (e.g. Dunham and Mikheyev 2010).

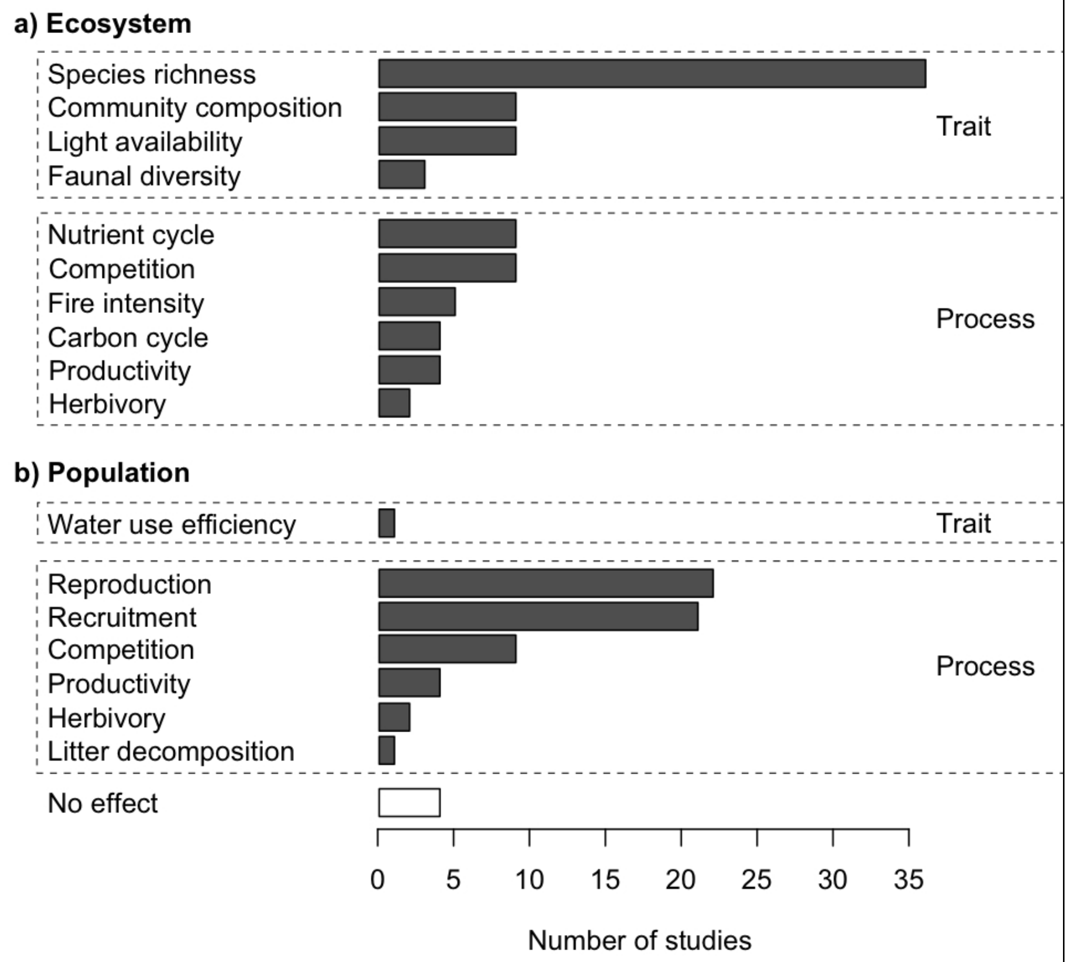

Figure 1: The effect of plant invasions on ecosystem properties in tropical forests. Both, the whole ecosystem (a) and single populations (b) can be affected. Note that some effects are mentioned in both categories. (n = 55 studies)

In addition to suppressing recruitment, invaders are reported for their competitive exclusion effect on native species, i.e. by strong competition for resources such as light or water (Mack et al. 2000; Cordell and Sandquist 2008; Friday et al. 2008).

Biological invasions in tropical forests may alter disturbance regimes, for instance by enhancing fire frequency or intensity. It was found that bracken fern and *Lantana camara* invasions can alter fire regimes in native ecosystems through greater fuel accumulation which affects fire intensity (Schneider and Fernando 2010; Sharma and Raghubanshi 2010). Ultimately, biological invasions in tropical forests can reduce the

above ground biomass production in the native stands (Asner et al. 2009; Kueffer et al. 2007). They accelerate C-cycling in the forest soils, and thereby depleting soil C stocks (Litton et al. 2008).
Exotic invaders are reported to experience less herbivory than native species in the invaded ecosystems in the tropics (Dietz et al. 2004). The same was reported from other ecosystems also (Lake and Leishman 2004).

Taken together, plant invasions in tropical forests are affecting various ecosystem properties, e.g. biodiversity, nutrient cycling and disturbance regimes.

Drivers of plant invasions in tropical forests

Drivers, i.e. processes that facilitate biological invasions, can be attributed to two classes (Lonsdale 1999): (1) related to the invaded ecosystem (i.e. invasibility) and (2) related to the invading species (i.e. invasiveness).

Most studies conclude that physical disturbances act as an effective agent to increase the invasibility of tropical forests (Figure 2). Interestingly, positive (Meyer, 1998; Fine 2002; Baret et al. 2008; Schneider and Fernando 2010) influences of disturbances are reported. That is, disturbances encourage invasion like other ecosystems (Knops et al. 1995; Kotanen et al. 1998; Ross et al. 2002; Buckley et al. 2003; Gelbard and Belnap, 2003). However, negative (Fairfax et al. 2009) influences of disturbances on invasion are reported, although the positive correlations clearly outweigh the negative correlations.

Different anthropogenic disturbances which are very common in tropics such as fire (Schneider and Fernando 2010), logging (Friday et al. 2008), land use changes (i.e. conversion of forests into agriculture, urbanization, pasture management) (Joshi et al. 2009) facilitate biological invasions.

Natural disturbances, such as wildfires, storm damage, flooding, drought, herbivory or predation, however, can facilitate invasions (Drake 1998; Horvitz and Koop 2001; Baret et al. 2008; Edward et al. 2009). Vice versa, inherent ecosystem properties such as shading or litter fall constrain invasions by increasing seedling mortality and decreasing growth of invaders (O'Connor et al. 2000; Garcia-Robledo and Murcia 2005).

Previously empty niches, i.e. the availability of a surplus of resources compared to the use by a native plant community, can explain the invasibility of tropical ecosystems (e.g. Garcia-Robledo and Murcia 2005).

This mechanism can be suspected to be of low importance in saturated tropical ecosystems that have evolved over long time periods. In addition, it is difficult to quantify even if measurement of empty niche space and its impacts on invasion were conducted (e.g. Kueffer et al. 2007; Baret et al. 2008; Cordell and Sandquist 2008; Friday et al. 2008; Kurten et al. 2008; Schumacher et al. 2009; Asner et al. 2010 etc.). However, most of the studies from our formalized search just made an interpretation based on their findings that the invasibility of the ecosystem might be enhanced due to the presence of plentiful resources or empty niche. Though, some studies did some measurement of empty niches and showed how it impacts on invasions in tropical forests which were more interesting. For example, Sharma and Raghubanshi (2010) measured the empty niches as the measurement of light intensity and soil moisture in the tropical dry-deciduous forests in India and found that *Lantana camara* invasion was stronger under conditions of high light and soil moisture availability. Cordeiro et al. (2004) found significantly higher germination rates of an invasive species in large gaps. More empty niches may be available the more isolated a system is, this explains why isolation of ecosystems increase the invasibility of these ecosystems (Drake et al. 1998; Meyer 1998; Bruehl and Eltz 2010).

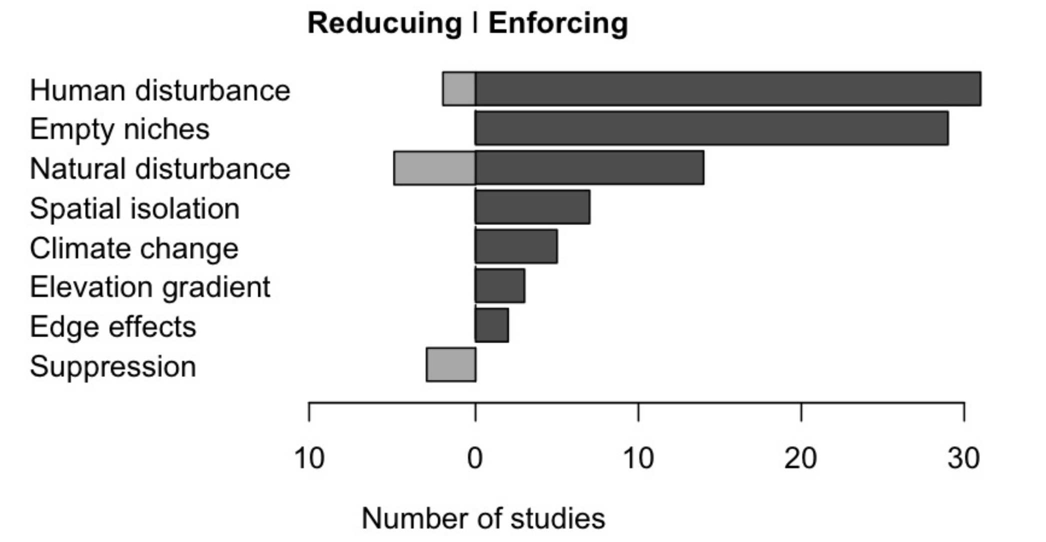

Figure 2: Different drivers characterize the invasibility of ecosystems in tropical systems as indicated by the investigated studies on biological invasions in tropical forests (n = 55 studies). Two drivers only represented in one study are not shown.

Generally, it can be expected that changes in the environmental regime are supporting changes in the invasibility of tropical forests. This leads to the availability of novel niches on one hand and to reduced competitiveness of established species on the other.

Global climate change and biological invasions are threatening the tropical forests through their mutual interactions (Wright 2005; Lewis 2006). For example, elevated CO2 increased the abundance, biomass of invasive species in the tropics (Litton et al. 2008; Raizada et al. 2009). Similarly, increased N-deposition facilitates the success of biological invasions in tropical forests (Asner et al. 2010). The same findings were also reported from other studies (Vitousek et al. 1987; Vitousek and Walker 1989; Dukes and Mooney 1999; Dukes 2002).

The ongoing fragmentation of habitats in the tropics as a consequence of land use changes is increasing edge effects (non-saturated species assemblages) and these are supporting invasion (Joshi et al. 2009). It was found that different management mechanisms (e.g. root trenching, regular burning etc.) can decrease the invasibility of tropical forests (Fensham and Fairfax 2006; Kueffer et al. 2007).

The control of invasives can be efficient, but it takes a lot of effort to achieve success. Dominance and biomass of non-native species were significantly decreased through intensive weeding activities in Hawaiian lowland wet forest (Cordell et al. 2009). Such kinds of approaches are unlikely to be affected in developing countries.

Elevational gradients within landscapes are providing specific opportunities for invasion because they offer a broad range of ecological conditions that apply to a variety of potential invasives (Dietz et al. 2004; Asner et al. 2009). In many cases higher elevated areas (especially mountains) have always been geographically more isolated from comparable ecosystems. They are thus often less saturated than lowland ecosystems and provide more available ecological niches (Steinbauer et al. subm.). However, depending on the geographical setting, this is not always the case.

Exotic species with broad environmental tolerance and high dispersal rates are the most successful invaders in tropical forests (Figure 3). Mode of dispersal plays an important role for the invasiveness (Rejmanek and Richardson 1996; Lake and Leishman 2004). Exotic invaders are furthermore reported to produce more numerous seeds combined with increased seed longevity than native species (Drake 1998; Fourqurean et al. 2010).

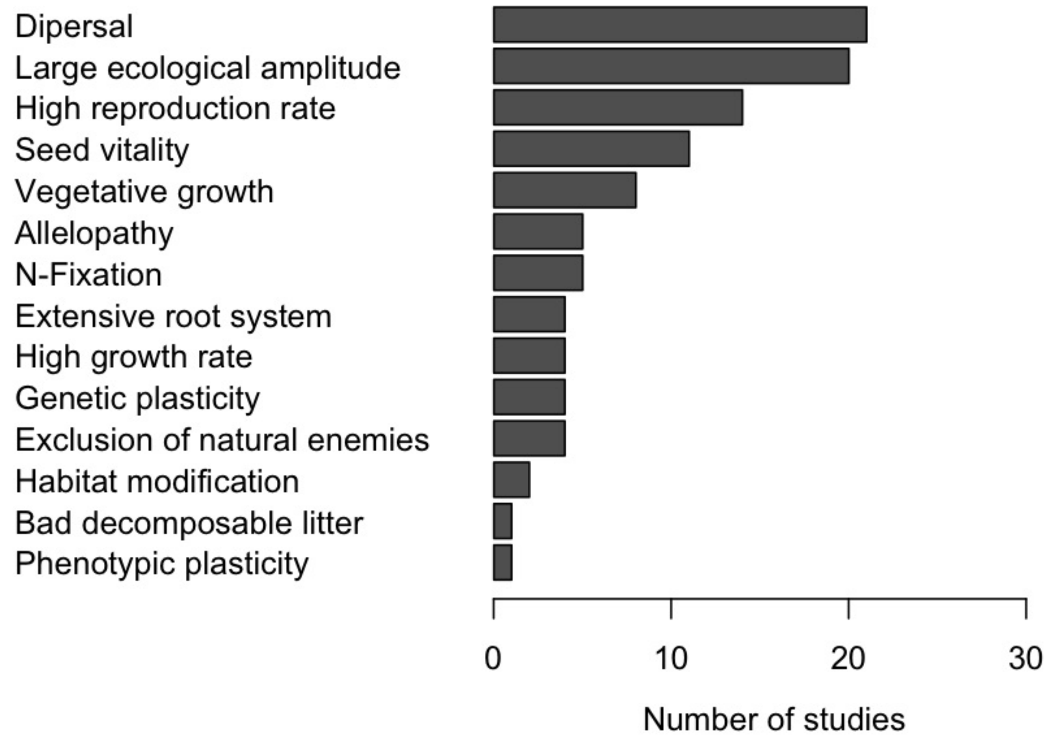

Figure 3: Characteristics that support the invasiveness of a species in tropical systems are indicated by the studies on biological invasions in tropical forests (n = 55 studies).

Some studies indicate that fast vegetative growth rates and vegetative regeneration strongly facilitate rapid spread of invasive species in tropical forests (Lichstein et al. 2004; Rodrigues et al. 2006; Fischer et al. 2009). The attribute vegetative propagation contributes to the success of exotic species invasion in different ecosystems (Henderson 1991; Rejmanek 2000; Lake and Leishman 2004). In addition, litter decomposition and N-fixation are two attributes which can increase invasiveness (Kueffer et al. 2008; Kurten et al. 2008). Highly decomposable litter and N-fixation increase the invasiveness of pioneer invasive species mainly in nutrient-poor soils. In the Hawaii Volcanoes National Park, an introduced small tree, *Myrica faya*, native to the Canary Islands, alters ecosystem-level properties and ecosystem development in young nitrogen-poor volcanic soils because of its high nitrogen fixing properties, thereby facilitating further invasions (Vitousek et al. 1987; Vitousek and Walker 1989). On the other hand, chemical toxicity of invaders leaf litter induces allelopathic effects on native species and increase invasibility (Davies and Boulton 2009). Some exotic species actively exude allelochemicals which are highly inhibitory to native plant species in the recipient communities (Hoffmann and Haridasan 2008; Sharma and Raghubanshi 2010). By such means, invasive species modify the habitat through altering the trophic structure, creating effective dispersal barriers for native species etc. (Bruehl and Eltz 2010). Though Fischer et al. (2009) show that habitat modification by invasive *Cinchona* even facilitate endemic species.

Invasive species are reported to exhibit more extensive root systems and higher specific leaf area than native species, thus enabling superior capture of resources such as light, soil nutrients or soil moisture (Kueffer et al. 2007). Invasive species furthermore benefit from plastic responses to sudden increases in light availability as a result of physical disturbances (Pattison et al. 1998; Davidson et al. 2011).

Generally, plants in the tropics are strongly controlled by highly specialized herbivores (Dietz et al. 2004). Release from such specialized natural pests in the new environment could therefore be a major explanation of invasions success in the tropics, as indicated by facilitated growth, abundance and habitat expansion of invasive species (DeWalt et al. 2004; Garcia-Robledo and Murcia 2005; Fourqurean et al. 2010).

There are some indications that successful invaders in tropical forests are characterized by high genetic plasticity, giving them the potential for rapid evolutionary change (Dawson et al. 2009a; Davidson et al. 2011). The number of studies in tropical forests, however, is not yet sufficient to explore this aspect in detail.

Hypotheses on plant invasions in tropical forests

Several hypotheses (29) have recently been formulated to explain the success of biological invasions (Catford et al. 2009). However, all of these have been postulated based on three major characteristics being influenced by humans; propagule pressure, abiotic and biotic characteristics. Here, we use the more structured and biogeographical classification of such hypotheses based on these characteristics provided by Hierro et al. (2005) for exploring which theories are supported by the case studies from the tropical forests.

The result is clear – the disturbance hypothesis and the empty niche hypothesis are well supported in the tropical forests, while other hypotheses are highly controversial with regard to findings (e.g. diversity hypothesis) (Figure 4). However, while the majority of studies report a positive relation between disturbance regime and invasibility, there are cases where e.g. fast-growing introduced species invade nutrient-poor, undisturbed habitats with low resource availability (Schumacher et al. 2009). More than half of the studies that are dealing with the empty niche hypothesis were conducted on islands (both continental and oceanic). Due to the specific characteristics of islands (e.g unsaturated species pool; low competitive ability of natives; lack of invader-specific herbivores and pathogens), island ecosystems are expected to be more invasible (Elton 1958; Lonsdale 1999) and a comparison to mainland systems is difficult.

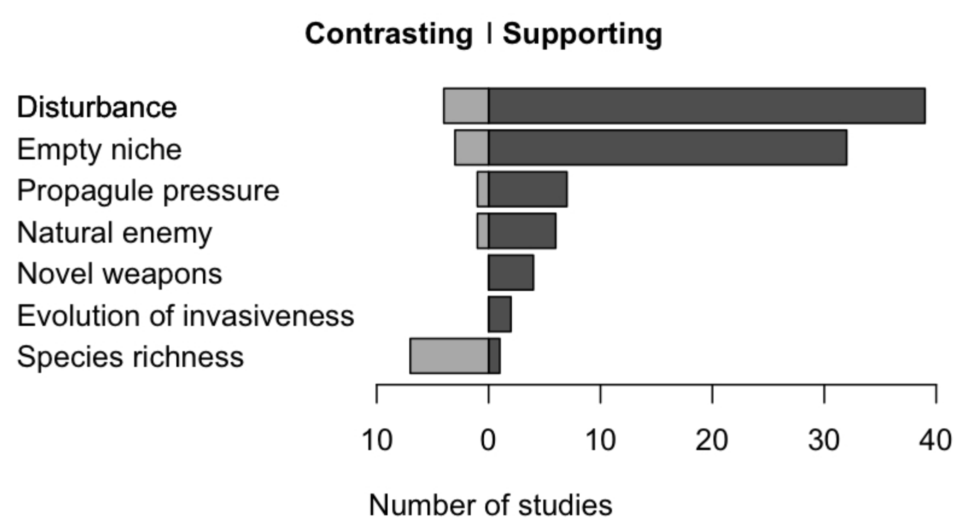

Figure 4: Formulated hypotheses (according to Hierro et al. 2005) are supported to a different degree by the investigated studies on biological invasions in tropical forests (dark grey bars orientated to the right). Some even mention contrasting results (light grey bars orientating to the left) (n = 55studies).

A certain degree of propagule pressure is necessary for any biological invasion (Drake 1998; Meyer 1998; Colautti et al 2006; Edward et al. 2009). Its relative role as compared to disturbance and empty niches, however, is not emphasized by the studies carried out up to now. As indicated above, the enemy release hypothesis could be of high relative importance in the tropics due to the highly specialized herbivory (Dietz et al. 2004). However, Dawson et al. (2009b) found no relationship between the enemy release hypothesis and exotic plant species invasiveness in their meta-analysis. They argued that more-invasive species were planted more than less-invasive species. Colautti et al. (2004) found the enemy release hypothesis mainly supported by biogeographical studies, while most of the community based studies either opposite or don’t support predictions of the hypothesis. Agrawal and Kotanen (2003) argued that the enemy release hypothesis might not be effective if the exotic species are close relatives of the native flora. In a common garden experiment they observed that exotics suffers comparably more from equal levels of leaf herbivory than the natives. Research on this aspect is needed in tropical forests.

The novel weapons hypothesis is based on increased invasion due to allelopathy (Hierro et al., 2005). Several studies support this hypothesis in tropical forest invasions (O’Connor et al. 2000; Tassin et al. 2009; Sharma and Raghubanshi 2010). As this is a recent hypothesis, the degree of support appears high in comparison to findings from other climatic regions. Allelopathy may therefore be of special importance in tropical forest systems.

Evolution of invasiveness, i.e. exotic invaders with the potential of rapid genetic changes, has already been discussed above. No general difference between tropical forests and other biomes is detected up to date, potentially due to the limited number of studies on this aspect (Dawson et al. 2009a; Fourqurean et al. 2010).

Elton’s (1958) biodiversity-stability (or biodiversity-invasibility) hypothesis is one of the oldest and most diversely discussed hypotheses concerning invasions. It proposes that species rich communities are more resistant to invasion than species-poor communities and is therefore related to the empty niche hypothesis. With regard to tropical forest invasions, our analysis resulted in mixed findings. Some studies support the hypothesis (Leung et al. 2009; Tassin et al. 2009) while others do not (Fischer et al. 2009). Generally, most large-scale observational studies find that communities with high species richness also contain many exotic species, i.e. a positive relationship between native diversity and invasions. Many experimental studies support the proposed negative relationship between biodiversity and invasion. This paradigm is referred to as the "invasion paradox" (Fridley et al. 2007).

All these results, however, may be biased by the available studies, as the study design limits the theories that could be tested. While only some studies aimed to test these hypotheses most only related their findings to them. Yet, theories developed in other parts of the world appear to be able to explain the observed invasions in tropical forests. The strong dominance of disturbance as driver of invasions and the high degree of invasive species able to exude allelochemicals, however, appears unique. The availability of empty niches as prerequisite of invasion is surprising based on the high native species richness and the long-term stability of the ecosystems. We explain this finding with the fact that most studies supporting the empty niche theory stem from unsaturated islands.

Representation of different tropical forest types

There is a clear geographic bias in the studies conducted on biological invasion in tropical forests (Figure 5). with the majority of studies stemming from continental and oceanic islands or archipelagoes (e.g. Society Islands, Hawaii Island, Indo-Pacific islands; Meyer and Florence 1996; Drake 1998; Meyer 1998; O'Connor et al. 2000; Meyer and Lavergne 2004; Cordell and Sandquist 2008; Litton et al. 2008; Asner et al. 2010; Chimera and Drake 2010) This followed the same trend of research in invasion ecology in the tropics (Loope and Mueller-Dombois 1989; Vitousek and Walker 1989; Walker and Vitousek 1991; Conant et al. 1997; Medeiros and Loope 1997; Fine 2002; Denslow 2003; Mack and D'Antonio 2003; Allison and Vitousek 2004). However, insights gained on islands, though important, might not be transferable to tropical mainland forests. Unsaturated species pools, low competitive ability of native species, lack of invader-specific herbivores and pathogens generally lead to increased invasibility of islands (Lonsdale 1999; Denslow 2003; Dewalt et al. 2004; Meyer and Lavergne 2004).

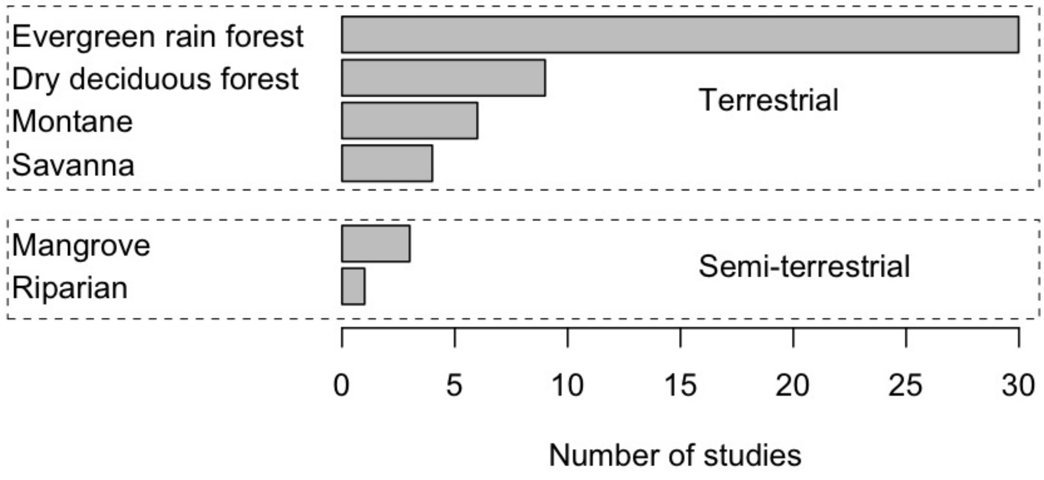

Figure 5: The number of studies on biological invasions differs between forest types. There is a clear biogeographical bias in invasion studies in tropical forests where most of the studies were conducted in evergreen rain forest. Two studies not fitting in the classification are not shown (n = 55 studies).

When classified according to Lewis (2006) it becomes obvious that different forest types are not equally well investigated with respect to biological invasions (Figure 4). Most studies have been conducted in tropical wet forests followed by tropical dry forests, savannah and montane forests. Few studies report on riparian forests (e.g. O'Connor et al. 2000). As this forest type is strongly driven by natural disturbances, it has to be assumed that invasion plays an important role. Mangroves, on the other hand, too, are scarcely studied with respect to invasions (Horvitz and Koop 2001; Liu and Pemberton 2009; Fourqurean et al. 2010). The highly selective abiotic environment and the almost global dispersal of the native tree species, however, imply that mangrove forests are not very susceptible to biological invasions.

Still, it is remarkable how little is known about biological invasions in tropical forests other than tropical wet forests. A modification of these ecosystems could affect the lives of millions of people who are depending on these ecosystems.

Conclusions and implications for future research

Studies on biological invasion of tropical forests are dramatically underrepresented in ecological research. Regarding as well the spatial extent as the biodiversity of tropical forests and the threats to these ecosystems by land use and climate change, the detected knowledge gaps are more than surprising.

Consequences of tropical forest invasions are manifold. Ecosystem or community structure (e.g. species richness, community composition, recruitment) of tropical forests can be altered by biological invasions. Effects on ecosystem properties and processes (e.g. nutrient cycling, carbon cycling, water balance) are scarcely investigated. However, incidental findings are indicating substantial consequences of biological invasions.

Theoretical concepts that have been developed in order to identify generality in invasion processes apply to a limited extent also to tropical forests. The empty niche hypothesis is supported by a number of studies. However, its verification in continental tropical forests is not yet supported by case studies and might differ from well studied tropical islands.

Successful tropical invaders do not differ in their basic traits - broad environmental tolerances, high dispersability and ability for vegetative regeneration - from other climatic zones. Until now there is little evidence for the role of genetic plasticity in tropical forest invasions.

Biological invasions in tropical forests are supported by physical disturbances and resource availability. The pressure of such impacts is increasing strongly in recent decades. Management can help limiting biological invasions in tropical forests. Yet, it is essential to first explicitly agree on management goals (conservation of native species compositions or securing ecosystem functioning and services).

Experiments on the interaction between climate change and biological tropical invasions are not established. Preferably, research on climate change effects should include different aspects of climate change, such as gradual warming, altered precipitation, extreme events.

Most research on biological invasions in tropical forests refers to wet tropical forests on islands. More research is needed in mainland forests and especially also in dry forests and mountain ecosystems.

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Exotic Plant Species in Bangladesh Forest Ecosystems

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Abstract

Exotic species are increasingly invading ecosystems. However, the knowledge on alien species is still limited in tropical systems in general and in Bangladesh in particular. Here we investigate exotic species in the Satchari Protected Area and its surrounding landscape, one of the few protected forest ecosystems in Bangladesh. Traits and the biogeographic origin of the non-native species in the study area are provided. Boosted Regression Trees and Detrended Correspondence Analysis are used to determine the contribution of various environmental variables including disturbances to explain the distribution of exotic species within the forest.

Species richness, elevation, disturbances and soil parameters associated with agriculture were identified as good predictors for the number of exotic species. In Satchari Reserved Forest, the number of alien species shows a hump-shaped relationship with native species richness. The relationship is negative in the surrounding area. An increase in invasive species with anthropogenic disturbances is detected in the study area. Protection status is reflected in the presence of exotic species with less invasive species in better protected areas.

Keywords: nature conservation area, non-native species, systematic sampling, tropical forest.

Introduction

Many ecosystems are exposed to the invasion of alien species making exotic biota increasingly important for ecology, conservation biology and biogeography (Underwood et al. 2004; Simberloff 2005). Biological invasions are perceived as one of the most important results of human-induced global environmental change (Lonsdale 1999; Prieur-Richard and Lavorel 2000; Fine 2002; Seabloom et al. 2006). Introduced species are considered to be problematic for high conservation value areas due to their detrimental effects. Furthermore, the conversion of habitats can threaten the persistence of wildlife.

Due to the speed of development, improved knowledge on exotic species is urgently needed, especially on their biogeographic and climatic distribution, mode of introduction and taxonomic pattern (Silva and Smith 2004). The relevance of disturbances, spatial scales, land use and native species has to be understood. Knowledge of processes that are promoting the establishment of exotic species is essential for the control and management of exotic plants in forest ecosystems, conservation areas and commercially-managed ecosystems (Hill et al. 2005). Recently, almost 30 hypotheses from the fast growing scientific field of invasion ecology were reviewed and integrated into a theoretical framework (Catford et al. 2009). However, empirical evidence on invasion processes and patterns in tropical ecosystems is very scarce.

As a consequence of its location, topography, and history, Bangladesh has been influenced by migration and dispersal for thousands of years. Traditional reference points in time such as 1492 (Columbus) do not apply to this region. Thus, the distinction of introduced and native species is not a trivial issue. So far, there is also no good record of introduced species in Bangladesh. Among those aliens known, herbaceous species and lianas are dominant, followed by trees and shrubs (Hossain and Pasha 2001). Some of the alien species have become invasive due to their luxuriant growth having a negative influence on native species (Hossain and Pasha 2001).

Bangladesh is one of the countries with highest population density in the world (1099.3 people km^{-2}). Its forests in particular are under tremendous anthropogenic pressure. The geographical setting makes the country vulnerable to natural disturbances such as floods, droughts, cyclones and storm surges, erosion and landslides etc. These anthropogenic and natural disturbances can act as a catalyst (Jentsch and Beierkuhnlein 2003) accelerating the establishment of alien species.

Most of the publications on non-native species in Bangladesh are in the form of simple enumerations listing names, sources of origin and occasionally possible effects (e.g. Barua et al. 2001; Hossain and Pasha 2001; Islam et al. 2003; Akter and Zuberi 2009). More detailed investigations of alien species including quantitative measures and the assessment of drivers and side effects are rare (Islam et al. 1999; Biswas et al. 2007).

In this study, we analyze alien plant species in a tropical forest ecosystem. The aims of our study are: a) to gain insights into the introduced flora of this tropical forest including its biogeographical origin, the mode of introduction, taxonomy and life-forms and b) to analyze the spatial distribution of exotic species in relation to disturbance characteristics, edaphic settings, topographic variables or native species richness.

Methods

Study Area

Satchari Forest Reserve and its surrounding environment is located in the north-eastern part of Bangladesh (between $24^0$5' and $24^0$9' N and $91^0$24' and $92^0$29' E). The study area covers 40 km^2 and is divided into the three distinct units Satchari Reserved Forest, Satchari National Park, and surrounding areas. Satchari Reserved Forest was declared a reserve in 1914 and recently (2005) part of the natural forest in this reserve was declared as Satchari National Park. Satchari is one of the last habitats in Bangladesh for Hoolock Gibbons (primate, *Bunopithecus hoolock*) and the rare Hooded Pitta (passerine bird, *Pitta sordida*). The region has been targeted for multiple types of plantations with non-native species such as *Acacia auriculiformis* and *Eucalyptus camaldulensis*. It also became known because of its extensive Oil Palm (*Elaeis guineensis*) plantations established in the mid seventies (Choudhury et al. 2004).

The study area has a sub-tropical monsoon climate with three distinct seasons viz., the dry summer (march to mid June), the wet monsoon (mid June to mid October) and the dry winter (mid October to February). Mean annual rainfall is 4160 mm. However, the annual precipitation varies considerably from year to year. The driest period is between December and March. Most precipitation occurs during the monsoon from June to September, whereas July receives the highest amount of rainfall (about 1250 mm). The relative humidity ranges from 74% in December to 90% in July and August. The mean minimum and mean maximum temperatures during January and May are 12^0C and 32^0C, respectively. Acidic soils dominate the area (sandy loam to silt clay) and the relief is characterized by a gently undulating to hilly topography. The altitude in the study area is generally low with hilltops reaching 104 m a.s.l. and increasing towards India with elevation reaching 144m a.s.l. beyond the border.

The climax forest of the study area has been classified as a mixed tropical evergreen forest (Champion 1936). Today, natural forests are almost entirely restricted to the Satchari National Park, while the rest of the study area is subjected to different levels of human disturbance. Some of these disturbed forest areas were converted extensively into agricultural fields, orchards, human settlements, sungrass fields and plantations. Most plantations are dominated by exotic species such as *Acacia spp*., *Eucalyptus camaldulensis, Tectona grandis, Albizia falcataria*.

Sampling design

Systematic sampling was applied to avoid any biased data collection (Figure 1). The Surrounding Area has a near to homogeneous vegetation structure that is dominated by tea gardens and fallow lands for example. There, the plot distance was set at 800 m, while for the other units viz. the Satchari Reserved Forest and the Satchari National Park, the plots were 400 m apart. The sample size as well as the sample adequacy (number) was based on previous analyses of species-area curves. All tree species were recorded using a circular sampling plot with a 10 m radius. Furthermore, herbs, grasses, climber species and shrubs were sampled in three nested (2 m x 2 m) square plots within each circular plot. In total, some 139 plots were sampled of which 88 were located in the Satchari Reserved Forest, 14 were located in the Satchari National Park core area and 37 in the surrounding areas. Locations were recorded by GPS for future comparison.

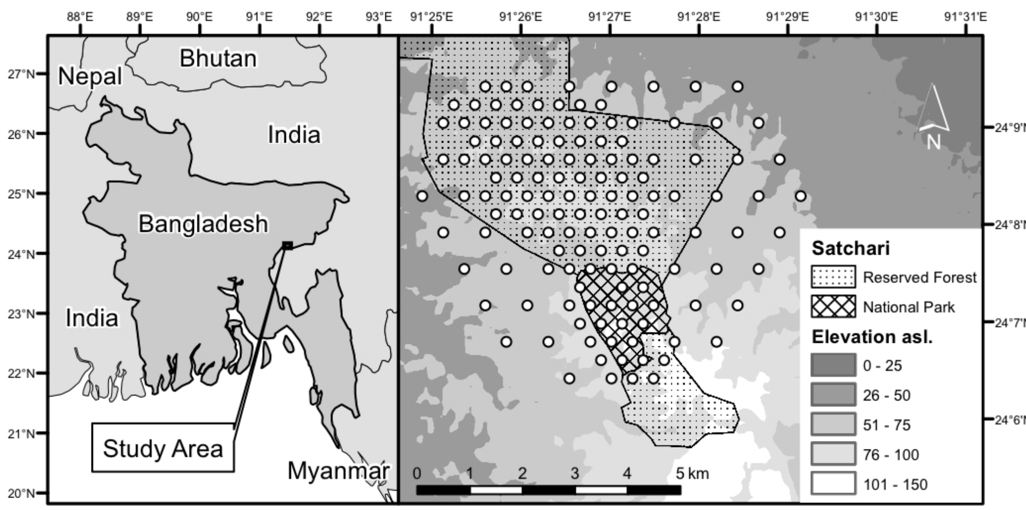

Figure 1: A stratified systematic spatial arrangement of plots (white circles, oversized) for the sampling of plant species and environmental data was applied in the study area in the eastern part of Bangladesh. The core area (shaded) of Satchari National Park is under higher protection compared to the Satchari Reserved Forest (dotted area). In the surrounding area outside the park, land use is dominated by tea plantations and settlements (from Uddin et al. subm.).

Biotic data

Families and genera were obtained from the Encyclopedia of Flora and Fauna of Bangladesh (Ahmed et al. 2008). To assess their biogeographic and climatic origin, any exotic species that were recorded in the study area were classified according to their continent of origin. For the biogeographic origin of aliens, five classes were defined: a) America (including North America, South America and Central America); b) Europe (including the Mediterranean areas of Asia), c) Africa (including Madagascar), d) Australia (including New Zealand) and e) Asia (excluding Bangladesh). A further sub-division separated temperate and tropical areas of origin.

The overruling climate was used for large biogeographic areas characterized by different climates resulting in a classification of a) tropical origin including Central and South America, Africa, Asia, Australia and b) temperate origin including North America and Europe.

If known, intentionally introduced species were grouped by their purposes of introduction based on Hossain and Pasha (2001) and Hossain (2003). Species were the purpose of introduction is unknown, where additionally classified if they are now considered as weeds. An overview of the number of alien species in different taxonomic ranks is provided. In addition, plant life-forms were determined following Ellenberg and Mueller-Dombois (1967).

Environmental variables

Elevation, inclination, aspect sinus (relative east aspect) and aspect cosinus (relative north aspect) were derived from a digital elevation model (ASTER; ESRI 9.3; data Void filled) based on the GPS locations.

The edaphic variables bulk density, pH, moisture content, soil organic carbon, available P, Ca, Mg and K were measured. Five soil samples (0-30 cm depth) were collected from each circular plot. All soil samples of one plot were homogenised. A portion of the composite soil sample (ca. 350 g) was air-dried at room temperature (20-25°C) for 7-14 days. The air-dried soil was sieved to 2 mm and analysed for soil organic carbon, available P, Ca, Mg and K in the analytical laboratory of Bangladesh Soil Resource Development Institute. The 'Core method' was used to the calculate bulk density and the pH of the soil sample was measured in a 1:2.5 soil-water suspension. Another part of the soil was stored for some weeks in closed polythene bags and weighed. This soil was then oven-dried at 105°C for a period of 24 h and weighted again to determine the antecedent moisture content. Soil organic carbon was determined by Walkey and Black's wet oxidation method. Bray and Kurtz' method was applied to determine the available P, while the flame photometer method was used for the available Ca, Mg and K in the sample.

Disturbance data were collected following the methodological framework proposed by Buhk et al. (2007) for plant diversity and disturbance regime assessment at the landscape level. For each plot, all detectable disturbances (Table 1) were recorded based on the following temporal and spatial descriptors: frequency (1/year, 2/year, >2/year), duration (<day, <weak, <year, >year), distribution (homogeneous or heterogeneous), form (punctiform, linear, laminar) and size (small, large). The number of disturbances as well as the number of different disturbance features were incorporated in the further analyses.

Data analysis

All analyses were performed using the free statistical software R version 2.10.0 (R Development Core Team 2009). In use were the packages “vegan” version 1.17-0 (Oksanen et al. 2010) and the package like “gbm” version 1.6-3 as provided in the appendix of Elith et al. (2008).

Boosted regression trees (BRTs) were applied to assess the relationship of explanatory variables with the number and the percentage of exotic species. All environmental and disturbance variables were included as predictors. Particular focus was given to: a) the relationship between exotic and native species, b) the effect of the environment (topographic and edaphic) on exotic species, and c) the effect of disturbances on exotic species. Boosted regression trees were calculated by function gbm.step (gbm 1.6-3) as provided in Elith et al. (2008). As implemented, cross-validation was used to determine the optimal model settings, while all data were used to fit the final model. The measure of the relative influence of predictor variables is based on the number of times a variable is

Table 1: Disturbance regime in the study area with 139 plots.	
Disturbance type	Frequency
trampling	127
fire wood collection	100
drought	94
storage and movement of fire wood	84
illegal logging	75
bamboo collection	46
disease and pest attack	43
dense leaf litter	40
storage of debris	37
water erosion	35
weeding	34
fertilizing	31
pruning	30
mulching	30
plucking (tea harvest)	30
ground fire	29
pesticides	27
storage of pruned materials	27
soil excavation	26
(annual-) trench rebuilding	25
sungrass collection	22
grazing	21
wind throw	19
forest cardamon collection	16
below ground tuber harvest	13
wind erosion	8
cane collection	6
wild boar	6
temporal standing water	5
palm seed collection	4
agricultural use	3
discharge of garbage	3
flower broom collection	3
thinning	3
infrastructure development	2
compaction by vehicles	1
farming	1
ploughing	1
sand collection	1

selected for splitting, weighted by the improvement of model results (see Elith et al. 2008). Final model settings were a bag fraction of 0.75, a Gaussian error distribution, a learning rate of 0.008 and a tree complexity of 2. The optimal number of trees resulted in 1100 and 1250 for the number and the percentage of exotic species, respectively.

The relation between the number of exotic and native species was separately visualised and analysed for the three protection units. Linear regression (with r^2 as goodness of fit indicator) was applied.

A Detrended Correspondence Analysis (DCA, Hill and Gauch 1980) was used to analyse the similarity of exotic species assemblages; to detect the relationship with environmental variables and disturbances; and to visualize the distribution of exotic species with respect to these environmental variables and disturbances. For this, we used the R-package “vegan” version 1.17-0 (Oksanen et al. 2010). Environmental variables were post-hoc fitted to the ordination using the function “envfit” in the same R-package. A permutation test with 10,000 iterations was applied to assess any significance. Only those variables ($p \leq 0.05$) that were relevant were shown.

Results

The exotic species

A total of 348 species occurred in the 139 sampled plots, 31 (8.9%) of which were non-native ones, which represent a considerable proportion of the introduced/non-native species in Bangladesh (Appendix S1). Most of the exotics had their biogeographic and climatic origin in the tropical areas of Asia and America followed by Australia and Africa (Figure 2a). Although there are strong colonial and commercial links between Europe and Bangladesh, Europe did not contribute to any of the non-native species found in the study area, due to a non-compatible ecosystem and climate. A high proportion of exotic species was introduced with the purposes of timber or firewood production (Figure 2b). For many species the mode of introduction is unknown, but the majority is now considered as weeds.

The majority of the non-native species were trees (48%). Trees were often introduced for the purpose of commercial timber production and the afforestation of degraded lands. A few of them were also introduced for fruit production (e.g. *Artocarpus heterophyllus, Cocos nucifera*, *Psidium guajava*, *Elaeis guienensis*). Most of the other species were widespread tropical weeds regardless of their habitat. A few alien species of medicinal value were also recorded, although their purposes of introduction were unknown or not medicinal.

Altogether, 31 exotic species comprising of 15 families and 28 genera were documented in the study area (Table 2). *Clerodendrum viscosum*, *Mikenia scandens*, *Eupatorium odoratum*, *Urena lobata*, *Imperata cylindrical*, *Lantana camara*, *Acacia auriculiformis*, *Eucalyptus camaldulensis*, *Melastoma malabathricum*, *Ageratum conyzoides*, *Mimosa pudica*, *Tectona grandis and Acacia mangium* were the most frequent exotic species. These species are also common in other forest ecosystems in Bangladesh (see Hossain and Pasha 2001; Barua et al. 2001; Islam et al. 2003; Biswas et al. 2007; Akter and Zuberi 2009).

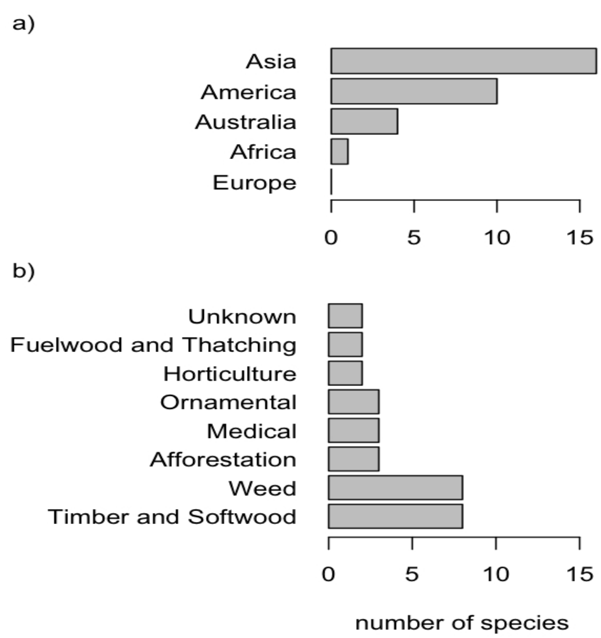

Figure 2: a) Biogeographic and climatic origin of exotic species in the study area
b) Purpose of introduction of exotic species in the study area

Table 2: Numerical summary of exotic plant species in the study area by taxonomic level and plant life-forms (Ellenberg and Mueller-Dombois, 1967)

	Pteridophyta	Gymnosperms	Angiosperms		Total
			Dicotyledons	Monocotyledons	
Family	0	0	12	3	15
Genus	0	0	25	4	29
Species	0	0	27	4	31
Phanerophytes	0	0	20	3	23
Hemicryptophytes	0	0	1	0	1
Therophytes	0	0	3	0	3
Lianas	0	0	2	1	3
Epiphytes	0	0	1	0	1

Most plant families are represented by only one species (Figure 3 a,b). However, *Asteraceae*, *Fabaceae*, *Malvaceae* and *Verbenaceae* constitute about 58% of the exotic flora. More than two-thirds of the exotic plant species in the study area are phanerophytes followed by therophytes, lianas, hemicryptophytes and epiphytes.

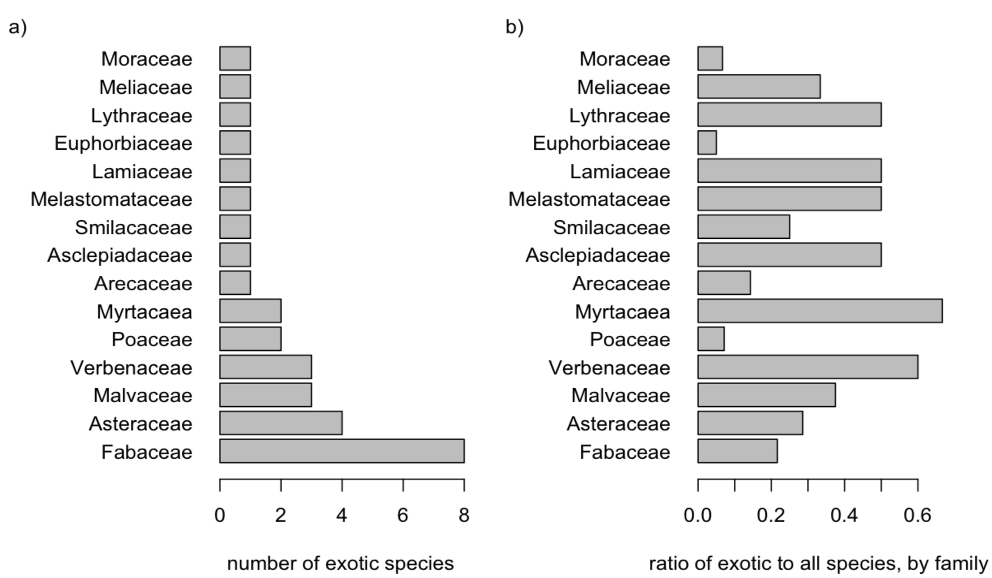

Figure 3: a) Major families of exotic flora and b) the ratio of the number of exotics to the total number of species per family recorded in the study area.

Relationship between native and exotic plant species richness

We found considerable differences in the native and exotic plant species richness among areas with different protection status in the study area (Table 3). Native species richness increases with protection status, while the number of exotic species decreases. Exotic species occurred in almost all plots (97%). The mean number of exotic species per plot was 4.4 (standard deviation 2.1). The number of exotic species in a plot is negatively correlated with native species richness (r = -0.19*). However, the relation is complex as can be seen in the boosted regression tree results as well as the separate analysis of the protection units (below).

Table 3: Native species richness and number of exotic species for areas under different protection status. Values are provided with standard deviations.

	Satchari National Park	Satchari Reserved Area	Surrounding Area
Species richness	38.6 ±15.6	22.6 ±11.0	13.1 ±5.5
Exotic species	3.3 ±1.7	4.3 ±2.1	5.8 ±1.8

Environmental variables and the distribution of exotic species

Predictive modeling based on boosted regression tree analyses (summary statistics provided in Table 4) reveals that the number of native species is the best predictor for both the number as well as the percentage of exotic species (Figures 4 a and b). The relationship between exotic species richness and total number of native species is unimodal. Native species richness explains 17% and 58% of the total variation for richness and the percentage of exotics, respectively. The percentage of exotic species declines with increasing native species richness. This can be expected from the reciprocal relationship of both values. Other environmental variables have less explanatory power. Both the number and the percentage of exotic species decline with elevation, but increase with phosphorus and the number of disturbances as well as bulk density.

Table 4: Summary statistics of boosted regression tree analysis for richness and percentage of exotic species.

	Number of exotic species	Percentage of exotic species
Mean total deviance	4.29	0.022
Mean residual deviance	1.18	0.003
Estimated CV deviance	3.34 (se: 0.35)	0.01 (se: 0.003)
Training data correlation	0.88	0.94
CV correlation	0.45 (se: 0.06)	0.76 (se: 0.06)

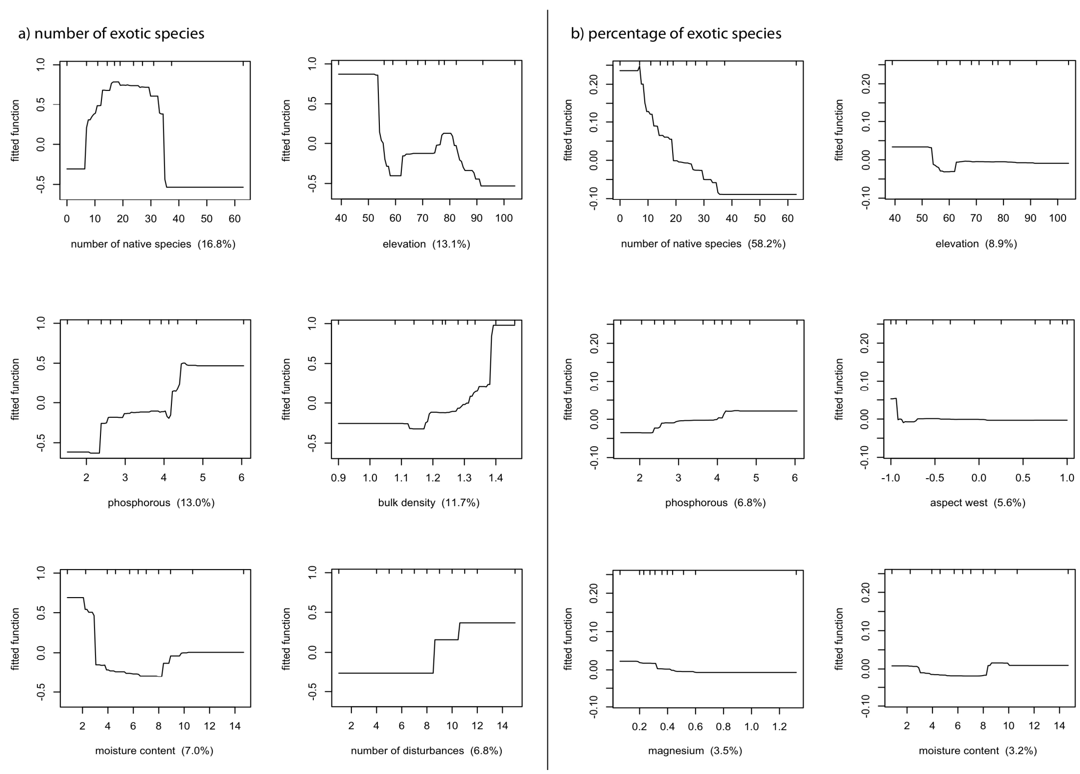

Figure 4: The first six most influential variables for the pattern of a) exotic species richness and b) the percentage of exotic species based on the results of the boosted regression tree models. Percentage values in parentheses demonstrate the relative amount of predictive variance explained by these variables alone from the total explained variance.

A closer look to the different protected areas reveals that the relation between the number of exotic species with the number of native species is linear negative (r^2: 0.18**) for the Surrounding area (figure 5a) but hump shaped for Satchari Reserved Forest (r^2: 0.18***; figure 5b). In the National Park no significant relation could be identified (figure 5c).

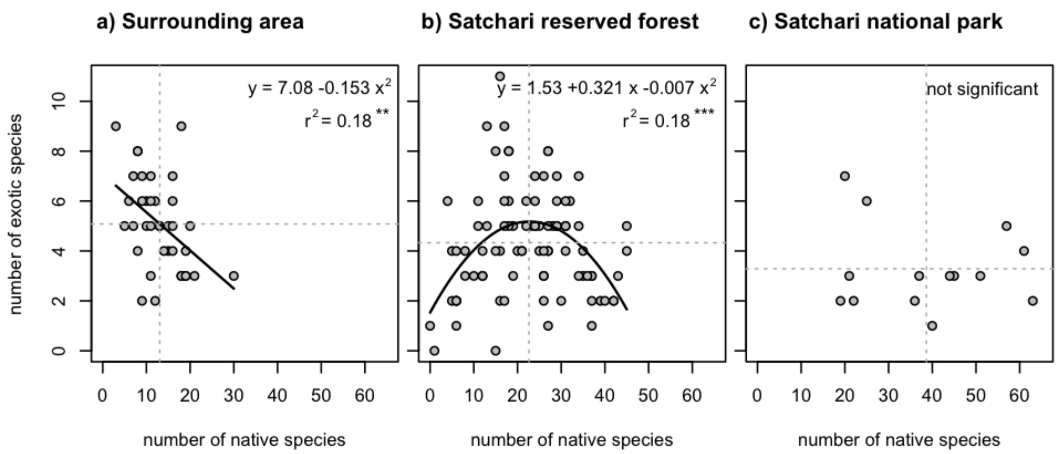

Figure 5: The relation between the number of exotic species and native species richness separated for the differently protected areas. Linear regressions reveal a negative relation for the Surrounding area (a) that is severely altered by human disturbances while a unimodal relation could be detected for Satchari Reserved Forest (b). No relation was found for the National Park core area (c), probably due to the lower number of samples.

Ordination by DCA reveals that the composition of exotic species assemblages is comparatively similar in the unprotected surrounding area, while a distinguished composition of exotic species was identified for plots in the Satchari Reserved Forest and in particular for the Satchari National Park (Figure 6). Thus, the composition of alien species varies more greatly in the protected areas. A gradient in the degree of protection is indicated along the first axis ($p<0.001$). This axis is related to four factors namely the number of disturbances, native and alien species richness, elevation and moisture content. With an increasing protection status, disturbance decreases and species diversity increases, while the number of alien species decrease.

Values indicating environmental conditions such as elevation and moisture also increase with protection status. Plots from the "surrounding areas" are associated with more disturbances and lower overall species richness but a higher number of alien species.

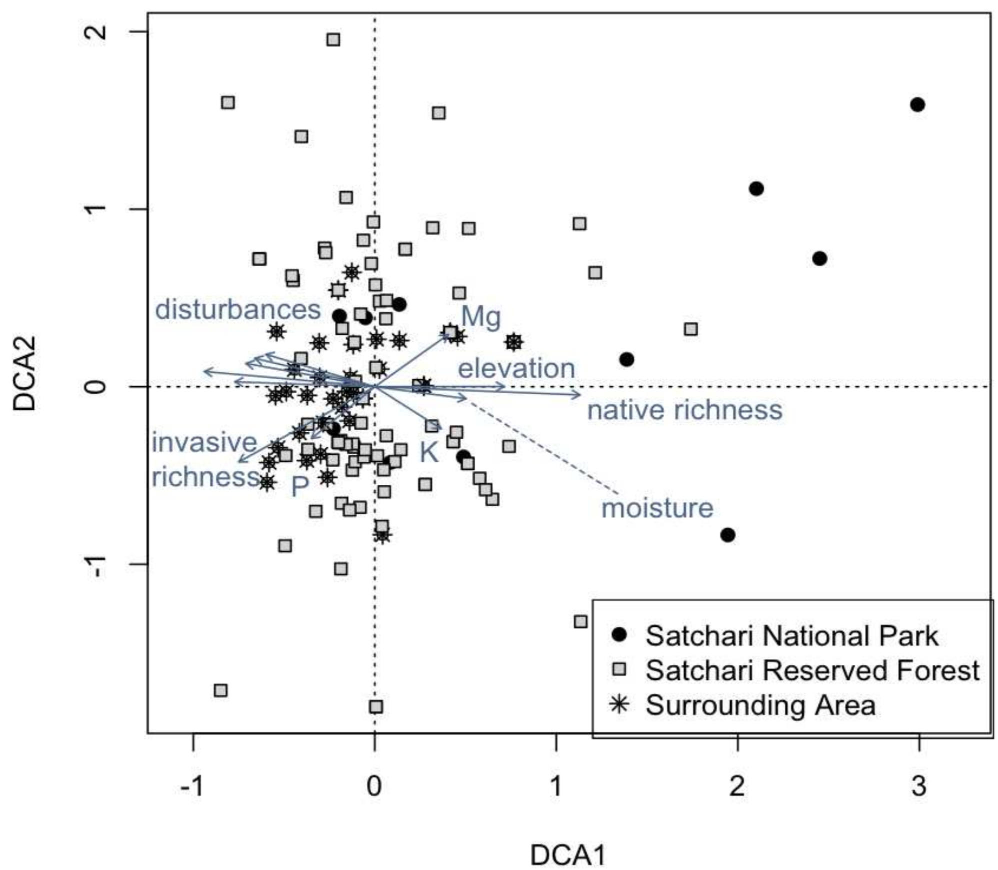

Figure 6: Biplot of DCA with sampled plots (points) for the exotic species recorded in the study area. Environmental variables were post-hoc fitted to the ordination and tested for significance using a permutation test with 10,000 iterations. Only relevant variables ($p \leq 0.05$) were visualised. The protection status is also significant ($p<0.001$) along the first axis, but group centroids are not shown. Explanations: n.spec = number of species, n.invas = number of invasive species, disturbances = from top to bottom: disturbance duration, size, distribution, overall number and frequency. Eigenvalues are 0.30 and 0.31 for the first and second axis, respectively, with a total inertia of 5.80.

Discussion

A large proportion (48%) of the alien species in the study area are trees. In the 19th and 20th Century valuable timber species and fast growing tree species were imported to facilitate the development of forestry in Bangladesh (Hossain and Pasha 2001; Islam et al. 2003). During the 20th Century, tree species of Australian origin were introduced. Most of the other exotic species are shrubs (16%) and herbs (13%). A large number of alien plants in the tropics are herbaceous and form weeds (Cowie and Werner, 1993; Hossain and Pasha 2001; Dogra et al. 2009).

Heywood (1989) indicated a correlation between the global size of higher taxa (e.g. family level) and the number of exotic species within these taxa. He found that the largest angiosperm families also supply a large proportion of exotics or invaders. Members of Poaceae, Asteraceae, Fabaceae and Brassicaceae represent most alien species in the world (Corlett 1992; Weber 1997; Pyšek 1998). Asteraceae and Fabaceae are the largest families of flowering plants in the world. In our analyses, Asteraceae and Fabaceae are also contributors to the largest proportion of exotic species in the study area. Most of the species were introduced mainly from the tropical areas of Asia and America, which is in accordance with the findings of other studies conducted in different parts of the tropics; species introduced from tropical origin adapt well in tropical destinations (Corlett 1992; Stadler et al. 2000).

We identified native species richness to be the most important predictor for both the number and the percentage of alien species. A decrease in the percentage of alien species with the number of native species is expected in any case assuming spatially regularly distributed exotic species richness and given the mathematical connection between both variables. For the relationship between exotic and native species richness, however, controversial results have been reported inducing a vivid debate referred to as the “invasion paradox” (Fridley et al. 2007). Fridley et al. (2007) found a mainly positive relationship between native and non-native species richness for studies conducted over broad spatial scales, while fine scales and in particular experimental settings support a negative relationship. The discussion is mainly based on the large number of studies in temperate systems. However, only a few investigations (Frayer 1991; Walker and Vitousek 1991; Turner and Tan 1992; Stadler et al. 2000; Fine 2002; Biswas et al. 2007) address the interrelationship between biodiversity and invasibility in the tropics. For the study area, exotic and native richness are significantly negative correlated. However, more detailed BRT results (figure 4) indicate a hump-shaped distribution showing an increase in the number of exotics along with native species richness peaking at around 15-20 species. Separate analyses for the differently protected areas (figure 5) reveal, the relation is negative in the disturbed areas surrounding the National Park while a hump shaped relation is detected within Satchari Reserved Forest. The low number of samples within the national park is probably the main reason for no significant relation here.

In spite of slight topographic differences in the area, the highest species richness is found in higher elevation plots (Uddin et al., subm.). As the higher plots are also located in better protected areas, the separation of protection and elevation is difficult. Furthermore, moist sites tend to support higher species richness. However, in the study area, the number of exotic species fall with a decline in disturbances. This fact, together with the protection status, indicates an increase in the invasive potential with human use. Some of the invasive species are known to be cultivated in the area surrounding the Satchari National Park (e.g. *Eucalyptus camaldulensis*, *Tectona grandis*).

In general, disturbed areas are suspected to support exotic species invasions (Lake and Leishman 2004). Disturbance events increase resource availability and reset succession, this increases the chance of colonization and establishment for many invasive species (Sher and Hyatt 1999; Colautti et al. 2006). Disturbance events can be natural (e.g. floods, cyclones, landslides) or anthropogenic (e.g. eutrophication, land use, clearing). However, up to date, disturbance-mediated invasion is suggested to be most effective when invaders are ruderals that are adept at primary succession (Catford et al. 2009), whereas in the study area most of the invading species are trees which are more adapted to early stages of a secondary succession. Lonsdale (1999) identified a positive relationship between human impact (the number of visitors and development) and exotic species richness in nature reserves. In the study area, the supply of phosphorus and bulk density is connected to higher numbers of exotic species. This indicates that land use intensity facilitates the introduction of alien species. Hill et al. (2005) identified the same pattern in an Australian woodland. Soil fertilisation was found to support exotic richness in various studies (King and Buckney 2002; Lake and Leishman 2004; Leishman et al. 2004).

Studies on the distribution and influence of invasive species in tropical ecosystems are rare and particularly in Bangladesh knowledge about this issue is still scarce, as most invasion studies have been conducted in temperate ecosystems.

Our results suggest that anthropogenic and natural disturbances support the establishment of exotic plant species in the forest ecosystems of Bangladesh. Nature protection in Satchari has shown to be not only an effective way of protecting species richness, but also for decreasing the chance for an introduction of non-native species.

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Supporting Information (Electronic Appendix for Manuscript 2)

Table S1: Name, origin and characteristics of the recorded non-native plants from Satchari Protected area. Abbreviations: In column "Scientific Name": 1= former remnants plantings; 2= self seeding/regenerated. In column "Family": D= Dicotyledons, M= Monocotyledons and P= Phanerophytes, H= Hemicryptophytes, T=Therophytes, L= Lianas, E=Epiphytes.

Scientific Name	Local Name	Family	Functional Group	Origin
Acacia auriculiformis [1]	Akashmoni	Fabaceae (D,P)	Tree (Afforestation)	Australia
Acacia hybrid (mangium X auriculiformis) [1]	Acacia hybrid	Fabaceae (D,P)	Tree (Afforestation)	Asia
Acacia mangium [1]	Mangium	Fabaceae (D,P)	Tree (Afforestation)	Australia
Ageratum conyzoides [2]	Fulkur	Asteraceae (D,T)	Herb (Weed)	South America
Albizia falcataria [1]	Malakana Koroi	Fabaceae (D,P)	Tree (Softwood)	Australia
Artocarpus heterophyllus [1]	Kanthal	Moraceae (D,P)	Tree (Horticulture)	Asia
Bombax ceiba [1]	Shimul	Malvaceae (D,P)	Tree (Softwood)	Asia
Cassia siamea [1]	Minjiri	Fabaceae (D,P)	Tree (Fuelwood)	Asia
Ceiba pentandra [1]	Kapok	Malvaceae (D,P)	Tree (Softwood)	Tropical America
Clerodendrum viscosum [2]	Bhat	Verbenaceae (D,P)	Shrub (Medicinal)	Asia
Derris trifoliata [2]	Derris	Fabaceae (D,L)	Climber (Unknown)	Asia
Elaeis guineensis [1]	Oil palm	Arecaceae (M,P)	Palm (Ornamental)	Africa
Eucalyptus camaldulenss [1]	Eucalyptus	Myrtaceae (D,P)	Tree (Timber)	Australia
Eupatorium odoratum [2]	Assampata	Asteraceae (D,H)	Shrub (Weed)	Tropical America
Hevea brasiliensis [1]	Rubber	Euphorbiaceae (D,P)	Tree (Timber)	South America
Hoya parasitica [2]	Pargacha	Asclepiadaceae (D,E)	Epiphyte (Unknown)	Asia
Hyptis suaveolens [2]	Tokma	Lamiaceae (D,T)	Herb (Weed)	Tropical America
Imperata arundinacea [2]	Sungrass	Poaceae (M.P)	Grass (Thatching)	Asia
Lagerstroemia speciosa [1]	Jarul	Lythraceae (D,P)	Tree (Ornamental)	Asia
Lantana camara [2]	Lantana	Verbenaceae (D,P)	Shrub (Ornamnetal)	Tropical America
Melastoma malabathricum [2]	Bon tejpata	Melastomataceae (D,P)	Shrub (Weed)	Asia
Mikania scandens [2]	Assamlata/ Germanlata	Asteraceae (D,L)	Climber (Weed)	Tropical America
Mimosa pudica [2]	Lojjaboti	Fabaceae (D,P)	Herb (Weed)	Tropical America
Psidium guajava [1]	Peyara	Myrtaceae (D,P)	Tree (Horticulture)	Tropical America
Saccharum spontaneum [2]	Kash	Poaceae (M,P)	Grass (Weed)	Asia
Smilax macrophylla [2]	Kumarialata	Smilacaceae (M,L)	Climber (Medicinal)	Asia
Spilanthes calva [2]	Surja kannya	Asteraceae (D,T)	Herb (Medicinal)	Asia
Swietenia macrophylla [1]	Mahagoni	Meliaceae (D,P)	Tree (Timber)	South America
Tectona grandis [1]	Teak	Verbenaceae D,P)	Tree (Timber)	Asia
Urena lobata [2]	Bon okra	Malvaceae (D,P)	Shrub (Weed)	Asia
Xylia dolabriformis [1]	Lohakath	Fabaceae (D,P)	Tree (Timber)	Asia

Biotropica, resubmitted after adapting the reviewer comments (ID-BITR-11-093)

Running head: Biodiversity in a Bangladesh Forest Ecosystem

The Influence of Habitat Characteristics and Nature Conservation on Biodiversity in a Bangladesh Forest Ecosystem

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ABSTRACT

Tropical forests are the hot spots of species richness on earth. Various impacts are increasingly harming these ecosystems. Improved knowledge on drivers, patterns and potential of protection attempts for the biodiversity of tropical forests is urgently needed in order to design and adapt management and conservation strategies in face of land use and climate change.

Because of the limited space and high population density, tropical forests in Bangladesh are especially under threat. Land use pressures and recent climate change compromises the conservation of the last (semi-) natural tropical forest ecosystems.

We conduct the first spatially explicit analysis of drivers and patterns of biodiversity in terrestrial Bangladesh forests based on multivariate approaches, similarity analysis and variation partitioning. Our aim is to differentiate the influence of soil type, topographic conditions, and disturbance regime as well as nature protection on plant species richness and heterogeneity patterns.

The study focuses on Satchari Reserved Forest and its vicinity. Plant species richness as well as species composition is strongly related to a disturbance gradient that is in correlated with protection and elevation (despite a small topographic range of 70 m). However, in our analysis both, topography and protection remain significant after correcting for disturbances. Soil characteristics are especially related to species composition, while only moisture has an effect on species richness. Results highlight the importance of disturbance regime, nature reserves and protected areas for biological diversity in Bangladesh. The enforcement of protection legacy and the integration of local communities have to be stressed.

KEYWORDS: Conservation, Disturbance Regime, Forest Reserves, Protected Areas, Reserved Forests, Sørensen similarity, Tropical Forests

ALTHOUGH TROPICAL FORESTS COVER LESS THAN 10% OF THE GLOBAL LAND SURFACE, THEY support the largest terrestrial biodiversity reservoir in terrestrial ecosystems and host more than 50% of all known plant species (Mayaux 2005). As tropical forests stretch through 50 countries around the equator, these ecosystems differ considerably in species composition, vegetation structure, biomass, spatial extension, abiotic site conditions and natural as well as anthropogenic disturbance regimes including land use (White & Jentsch 2001, Jentsch 2007). For many habitats in the tropics our knowledge on drivers and patterns of biodiversity at scale of landscape is limited, spatial studies are rare (Condit *et al.* 2000, Wright & Muller-Landau 2006, Kreyling *et al.* 2010).

Tropical ecosystems suffer increasingly from pressures that are induced by human land use and climate change (Peres *et al*., 2006; ter Steege 2010). This is especially true for Bangladesh, which is among the countries with the highest population density (1099.3 people per km^2) in the world. Protected areas are a common approach for the regulation of access and for the management of biodiversity. The establishment of protected areas is considered to be the most adequate way of protecting biodiversity in tropical systems especially for countries with a high pressure by human activities (Brooks *et al*., 2009). In Bangladesh, the responsibility for biodiversity conservation is not designated to a single institution but implicitly assigned to different state agencies (Kahn *et al*. 2008). Here, few attempts have been made to analyze biodiversity in forest ecosystems, its conservation status, and its drivers, which is crucial to conserve natural patches in this setting (Rahman *et al.* 2008). Former biodiversity studies in Bangladesh focused on indexing species (Alam 1988, Khan *et al*. 1994, Alam 1995, Hossain *et al.* 1996, Nath *et al.* 1998, Amin 2004, Uddin & Misbahuzzaman 2007) or on the diversity of species in home gardens (Miah & Hossain 2001, Alam & Masum 2005, Kabir & Webb 2008 a,b).

The objective of our study was to explore the spatial pattern in species richness and composition as well as to identify potential drivers of biodiversity in a Bangladesh forest ecosystem. The effect of nature protection was a special focus. Bangladesh has 2.53 million hectares of forest, covering 17.5% of its total surface (Ahmed *et al.* 2008). The hill forests of Bangladesh are dominated by tropical wet evergreen and semi-evergreen forests, which are restricted to Sylhet, Chittagong and Chittagong Hill

Tracts (Ahmed *et al.* 2008). However, only few floristic and community level studies are available (Alam 1988, Khan *et al.* 1994, Hossain *et al.* 1996, Nath *et al.* 1998).

We question, (1) how species richness pattern (alpha-diversity) in Satchari Forests is related to measurable environmental conditions and disturbance regime, particularly human land use. The high alpha-diversity of tropical forests has been studied extensively, but only scarce information is available for spatial heterogeneity and beta-diversity in tropical forests (Chave & Leigh 2002, Condit *et al.* 2002, Duivenvoorden *et al.* 2002; Palmer & Maurer 2005, Desalegn & Beierkuhnlein 2010, Kreyling *et al*. 2010). Therefore, we additionally question (2) whether spatial similarity in species composition can be linked to gradients in site conditions and land use. A special attendance will be given to the effect of (3) nature protection. It is hypothesised to have a positive effect on both alpha and beta diversity.

METHODS

STUDY AREA — The study was conducted in Satchari Reserved Forest and its surroundings. Located in the north-eastern part of Bangladesh, the area ranges between 24°5' and 24°9' N and 91°24' and 91°29' E and covers a surface of 40 sq. km (Fig. 1). The study area is representative for the hilly landscapes of Bangladesh in terms of vegetation, soils and topography. It has a monsoonal sub-tropical climate with precipitation falling almost entirely between June and September (Fig. 2). Mean annual precipitation (4162 mm) in the study area is suspected to be higher than at the next long term climate station in Srimangal (Choudhury *et al.*, 2004). July is the wettest month, with an average rainfall of about 1250 mm, while December is the driest month. The amount and distribution of rainfall in the wet season varies considerably between years. A number of sandy-bedded rivers are draining the forest. All of them dry out in winter but may expose some areas of forest to flash floods during monsoon. At that time the streams carry also large amounts of eroded substrate. The area has a gently undulating to hilly topography, which is typically formed with slopes and hillocks and is characterized by sandy loam to silty clay acidic soils. The altitude ranges from 30 m to 104 m asl.

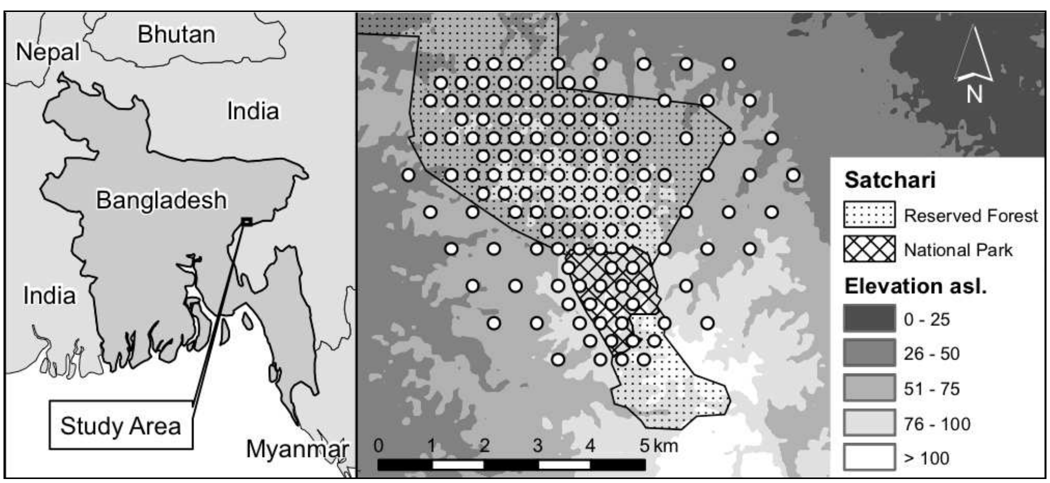

FIGURE 1: Location of the study area in Bangladesh and stratified systematic spatial arrangement of plots (white circles, oversized) with higher sampling density within the protected area. The study area is located close to the Indian border in eastern Bangladesh. Satchari National Park core area (shaded) is strongly protected. Satchari Reserved Forest (dotted area), parts of which are under protection. Outside the protected area, land use is dominated by tea plantations, fallow lands, and settlements.

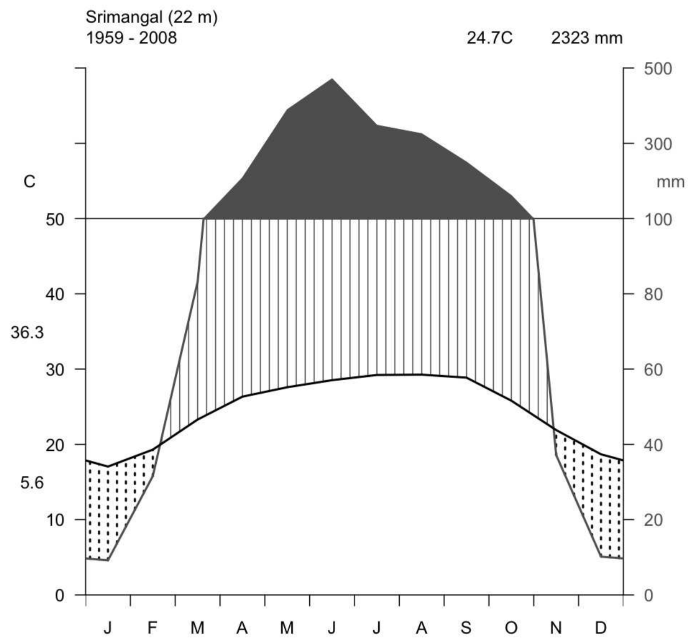

FIGURE 2: Climatic diagram (Walter & Lieth) of the Srimangal meteorological station. Srimangal meteorological station is ca.30km north-east of the study area and to our knowledge the closet station with long term meteorological records.

Climatic and edaphic factors of the study area are supporting tropical evergreen forests. The National Park, as a remnant of natural forests, has been protected against human disturbances to a great extent while the rest of the area is subject to human activities. There, almost all primary forests have been removed or substantially altered into secondary forests (Mollah *et al.* 2004). These human disturbances include tree harvest, plant material extraction (herbs, and fruits) but even illegal housing. Some of these disturbed forest areas were afforested with *Acacia spp*., *Eucalyptus camaldulensis*, *Tectona grandis*, *Albizia falcataria*, *Anthocephalus chinensis*, *Bauhinia acuminata* and some other species of minor importance (Mollah *et al.* 2004).

In Bangladesh, the protected area hosts the last habitats for hoolock gibbons (*Bunopithecus hoolock*) and the rare hooded pitta (*Pitta sordida*) (Choudhury *et al.* 2004). The area is known for its large number of bird species. The most abundant canopy trees are chapalish (*Artocarpus chaplasha*), jam (*Syzygium cumini*), belphoi (*Elaeocarpus floribundus*) and rata (*Canarium* spp.). The understory is typically comprised of shrubs such as airakuli (*Ardisia solanacea*), bonboroi (*Ziziphus oenoplea*) keya kanta (*Pandanus* spp.), assampata (*Eupatorium odoratum*) with a ground cover comprised predominantly by herbs. Almost all of the adjoining areas are tea gardens. However, Satchari has also become prominent in Bangladesh due to its vast oil palm plantations (*Elaeis guineensis*), which were raised in the mid seventies. This indicates the strong land use pressure in forest areas.

The study area is separated into three parts of different protection status: first Satchari National Park, second the Satchari Reserved Forest and third the direct vicinity that consists mainly of plantations. Satchari National Park is the protected core area within Satchari Reserved Forest. The enforcement of the protection status faces severe difficulties in Bangladesh especially due to a poor focus on public involvement in the protected area management process (Mukul *et al.* 2008), which has, however, recently been improved. Due to that especially Satchari Reserved Forest is exposed to several activities of illegal human impact.

SAMPLING TECHNIQUE — A stratified systematic sampling grid was implemented. The sampling was affected at a distance of 400 m between plots in those areas where a previously conducted remote sensing analysis indicated dense forest cover and at a distance of 800 m in the less dense forested surrounding areas (Fig. 1). The distribution of plots was fixed a priori in order to avoid investigator bias. Plots were arranged in a hexagonal grid that provides equidistance between neighbouring plots (see also Hassler *et al*. 2010). All tree species were recorded within a circular sampling plot of 10 m radius. In addition, three small (2 m by 2 m) quadratic units within each circular plot were installed in order to record herbs, grasses, climber species and shrubs. Altogether 139 plots were sampled.

At each plot three random soil samples were collected at 0-15 cm depth and merged to a mixed sample. After removing stones, pebbles and large pieces of plant material, soils were sieved by 2 mm mesh screen, stored in sealed polybags. Moisture content, pH, bulk density, total organic carbon, total nitrogen, available P, available Ca, Mg, and K were analysed. Bulk density was assessed by using the core method following

Islam *et al.* (2001). Soils were weighted for the purpose of moisture content determination. This weighted portion of the soil was then oven-dried at 105^{o}C for a period of 24 h and weighted again to determine the antecedent moisture content. Moisture content was measured two months after the sampling period from the stored polybags soils. Soil pH was measured in a 1:2.5 soil-water suspension with 1 M KCL (see Islam *et al.* 2001). Soil organic carbon was determined by Walkley and Black's wet oxidation method (Jackson 1958). Total nitrogen was estimated with the micro-Kjeldahl method by acid-digestion, distillation and titration (Page *et al.* 1982). Available P was determined according to Bray and Kurtz' method (Bray & Kurtz 1945). Available Ca, Mg and K were determined using a Beckman spectrophotometer with a standard flame attachment. Elevation, inclination, aspect sinus (relative east aspect) and aspect cosinus (relative north aspect) were derived from a digital elevation model (ASTER; ESRI 9.3; data Void filled).

The disturbance regime was assessed following Buhk et al. (2007). For each plot, all detectable disturbances (Table 1) were recorded. Each disturbance was characterised by temporal and spatial descriptors: frequency (1/year, 2/year, >2/year), duration (<day, <weak, <year, >year), distribution (homogeneous or heterogeneous), form (punctiform, linear, laminar) and size (small, large). The number of disturbances as well as the number of different disturbance features was incorporated in the further analyses (e.g. a plot with three different disturbances where two have the same frequency would get a frequency value of two).

Table 1: Disturbance regime in the study area with 139 plots.

Disturbance type	Frequency
trampling	127
fire wood collection	100
drought	94
storage and movement of fire wood	84
illegal logging	75
bamboo collection	46
disease and pest attack	43
dense leaf litter	40
storage of debris	37
water erosion	35
weeding	34
fertilizing	31
pruning	30
mulching	30
plucking (tea harvest)	30
ground fire	29
pesticides	27
storage of pruned materials	27
soil excavation	26
(annual-) trench rebuilding	25
sungrass collection	22
grazing	21
wind throw	19
forest cardamon collection	16
below ground tuber harvest	13
wind erosion	8
cane collection	6
wild boar	6
temporal standing water	5
palm seed collection	4
agricultural use	3
discharge of garbage	3
flower broom collection	3
thinning	3
infrastructure development	2
compaction by vehicles	1
farming	1
ploughing	1
sand collection	1

CALCULATIONS—Variables were correlated with species richness (Pearson's product moment correlation; R-function: cor.test). Significance was tested using F-test statistics. Significance values are indicated using ‘***’ for $p<0.001$, ‘**’ for $p<0.01$ and ‘*’ for $p<0.05$ in all analyses. Environmental variables were soil parameters (pH, N, Ca, Mg, K, P, bulk density, moisture content, organic carbon) as well as topography (elevation asl, aspect cosinus, aspect sinus, inclination) and disturbances (overall number and number of different classes in frequency, distribution, size and duration). Differences in species richness between the three classes of protection status (Satchari National Park, Satchari Reserved Forest and surrounding areas) were tested for significance using t-test.

To differentiate the joint and independent explanatory power of “moisture content” “elevation asl”, “protection status” for the species richness pattern from the effect of disturbance characteristics, a variation partitioning was conducted using multiple linear regression models (linear regression and adjusted r^2 as the goodness-of-fit measure; as implemented in the function varpart (R-package”vegan” version 1.17-0 Oksanen *et al.* 2010) following the guidelines of Legendre (2008). Variables explaining less than 0.5% ($r^2<0.005$) were omitted from illustrations in the figures.

A second aim was to identify whether the similarity in species composition (species turnover or beta-diversity or "differentiation diversity" sensu Jurasinski *et al.* 2009) is linked to environmental circumstances, topography and disturbance characteristics. The gradient length in ordinations is a valid measure of species turnover and "differentiation diversity" (Jurasinski *et al.* 2009). In a first approach, Detrended Correspondence Analysis (DCA, Hill & Gauch 1980) was applied to test the influence of variables under study on species composition using R-package ”vegan” version 1.17-0 (Oksanen *et al.* 2010). Variables under study were post hoc fitted to the ordination using function “envfit” in the same R-package. To differentiate the effect of environmental variables and protection from the influence of the disturbance regime, a partial Constrained Correspondence Analysis (CCA) with condition on disturbances (partial after removing variation caused by disturbance variables) was applied. In a second approach, the explanatory power for species composition of the variables under study was differentiated using variation partitioning as implemented in the function varpart (decomposition of RDA models; R-package ”vegan” version 1.17-0 Oksanen *et al*. 2010) following the guidelines of Legendre (2008).

Additionally we investigated the “uniqueness” of plots in terms of species composition. Uniqueness is calculated for each plot by taking the mean value of a comparison to all other plots in the survey (based on Sørensen similarity). The resulting values were tested against differences in measurable environmental circumstances and topography. The test was performed with Pearson's product moment correlation. Similarity in species composition was calculated with the Sørensen Index. This index offers comparability to other studies, but it is not independent from species richness (Baselga 2007). Thus we measure gradients in species turnover and nestedness. For further information on similarity indices refer to Koleff *et al.* (2003) and Tuomisto (2010 a,b). Similarity indices were calculated by using R-package ”simba” version 0.2-5 (Jurasinski 2007).

Cluster analyses (single linkage) for the Sørensen similarity reveals strong tendencies towards “chaining”. As this indicates gradients rather than discrete classes in species composition, a classification of the plots based on species composition is not reasonable.

RESULTS

SPECIES RICHNESS — We recorded a total of 348 species in 139 plots (Fig. 3a). The majority of the species encountered in the survey were trees (144 species) followed by herbs (73 species), shrubs (40 species), climbers (51 species), grasses (28 species) and epiphytes (12 species).

Spatial variations in soil parameters were rather small. Only “moisture content” had a significant but small correlation with the species richness pattern (r^2 = 0.11***). Consequently, the species richness pattern was fairly independent from soil parameters. Elevation (between 39m and 104m asl) had a significant positive correlation with species richness (r^2 =0.21***), tree species richness (r^2 = 0.28***), climber species richness (r^2 = 0.07**), epiphyte species richness (r^2 = 0.05*) and herb species richness (r^2 = 0.03*), whereas species richness was independent from inclination and aspect. Thus, there was a slight increase in diversity towards the hilltops. Species richness was found to decrease with the number of disturbances. Disturbance size was the best predictor (r^2 = 0.33***), followed by the overall number of disturbances (r^2 =0.29***), distribution (r^2 =0.27***), duration (r^2 =0.21***), frequency (r^2 =0.17***). All disturbance characteristics were highly collinear.

Large parts of Satchari protected area, including the core area, were covered by the study (Fig. 1b). The three different landscape units viz. Satchari National Park, Satchari Reserved Forest and the surrounding areas varied considerably in terms of species composition and richness (Fig. 3).

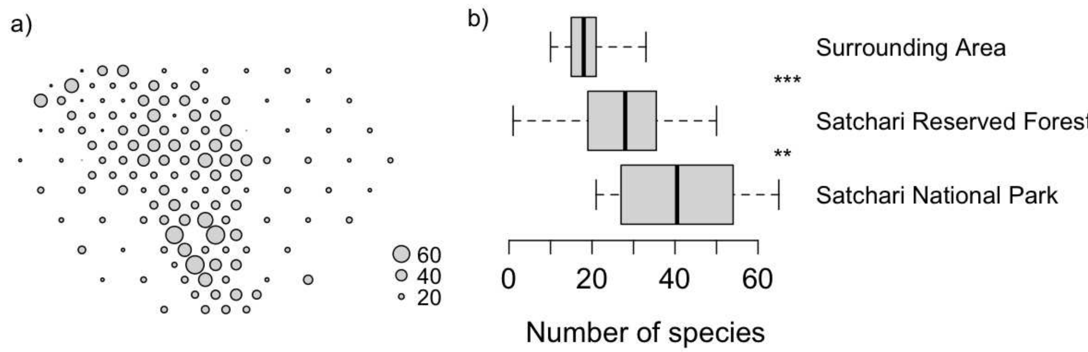

FIGURE 3: a) Species richness in the 10m radius plots. b) Plots with a higher protection status host significantly more species (t-test). Values in brackets indicate the number of plots in each class

Especially the plots sampled in Satchari National Park were relatively elevated (ranging from 69m to 104m; mean 89m ±10m asl), while those in Satchari Reserved Forest (ranging from 49m to 102m; mean 73m ±11m asl) and the surrounding area (ranging from 39m to 97m; mean 63m ±15m asl) were more or less normal distributed along the whole topographic range. Figure 4 illustrates the increasing species richness with elevation and the position of protected plots.

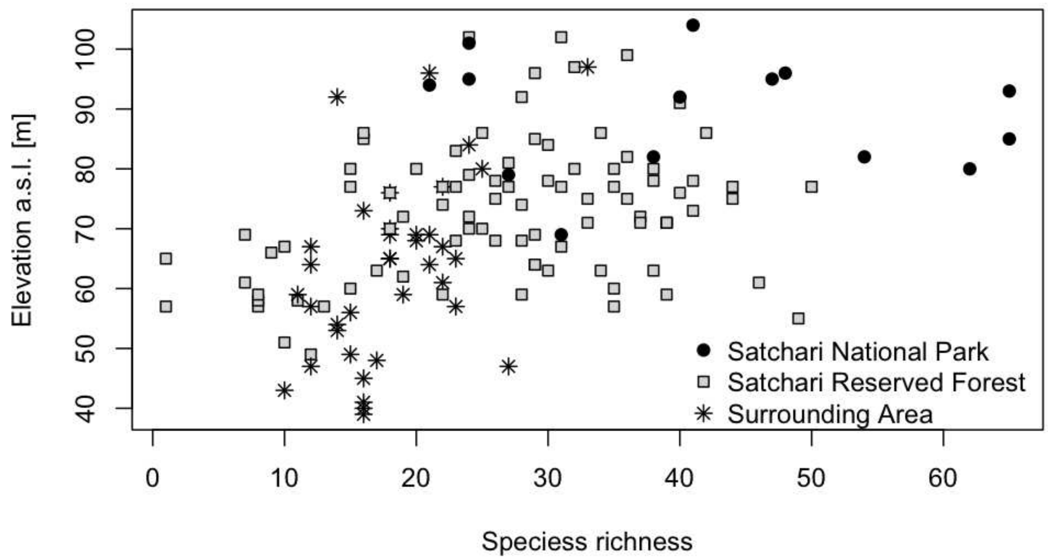

FIGURE 4: Species richness is increasing with elevation. However, the plots within the park also tend to be in higher altitude. Protection status is thus not independent from elevation.

Variation partitioning showing the overlap in explanatory power of elevation, protection status, soil moisture content and disturbance regime for the species richness pattern reviled that 65% percent of total explained variation (46%; adjusted r^2 of 0.46) can be explained by more than one investigated variable (Fig. 5). 22% of explained variation was jointly explained by disturbance regime, protection status and elevation. Only 13% of explained variation was independent from the disturbance regime.

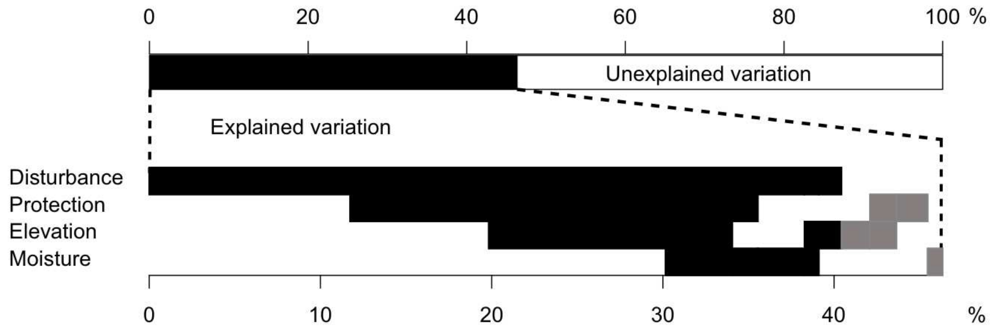

FIGURE 5: Variation partitioning based on linear regression reveals that a large fraction of explained variation of species richness is shared by disturbance regime, elevation and protection status. The independent contribution of moisture is comparable to that of elevation. The black and grey bars illustrate the variation in species richness explained by the variables. White spaces indicate percentage of variation explained by another variable but not the focal one. Only those variables with a significant relation to species richness were considered. Shaded in grey is that part of variation that can be explained without collinearity with the disturbance regime.

FLORISTIC COMPOSITION— The first DCA-axis revealed a similarity gradient from plots in Satchari National Park (on the left of Fig. 6a) over the plots in the Satchari Reserved Forest (medium protection status) to those plots in surrounding areas outside the reserve and the park (on the right of Fig. 6a). The first and second DCA axes (representing species turnover or beta diversity) were significantly related to protection (r^2 = 0.47***), elevation (r^2 = 0.27***), Mg (r^2 = 0.16***), moisture content (r^2 = 0.13***), pH (r^2 = 0.14***), P (r^2 = 0.11***), organic carbon (r^2 = 0.09***), N (r^2 = 0.07**), the number of disturbances (r^2 = 0.58***), disturbance duration (r^2 = 0.47***), disturbance size (r^2 = 0.23***), disturbance distribution (r^2 = 0.22***) and disturbance frequency (r^2 = 0.17***).

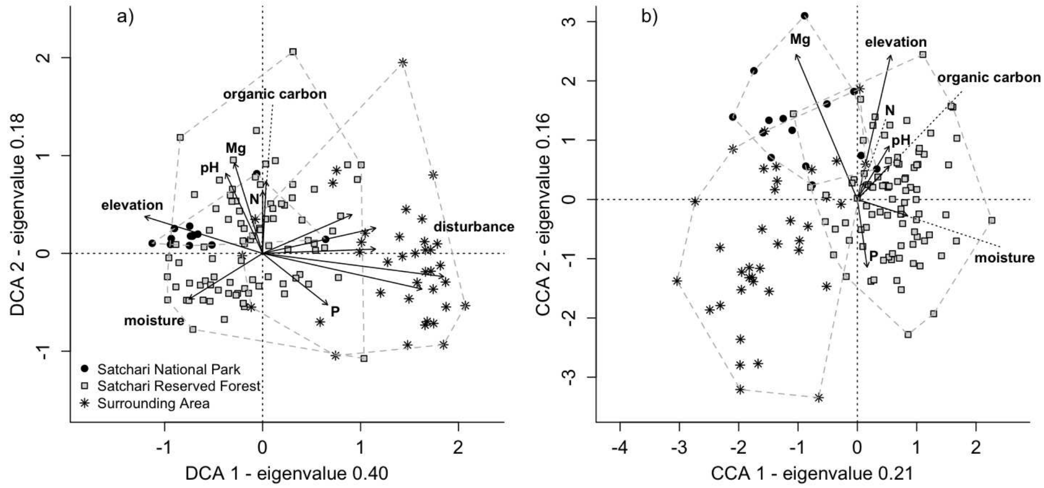

FIGURE 6: (A) A “protection” gradient is revealed by the first axis of the Detrended Correspondence Analysis (DCA). Protection status is indicated by the symbols. This gradient is also in strong collinearity with both elevation and disturbance characteristics (from top to bottom: disturbance - frequency, size, distribution, number and duration). (B) After removing the effect of the disturbance regime in a partial CCA the protection gradient shifts to the second axis. The fist axis is related to soil moisture and organic carbon.

After removing the effect of disturbances, the partial CCA (Fig. 6b) revealed the "protection gradient" on the second axis (beforehand on the first axis of the DCA) but not as distinct. The first axis was mainly related to the soil properties moisture and organic carbon. Partial RDA supported this interpretation (Figure 7). Disturbance regime (in collinearity with other variables) accounted for 65% of the overall explained variation (r^2 =0.11, 11%). Protection, elevation and soil variables alone accounted for 21%, 6% and 8% of the overall explained variation, respectively.

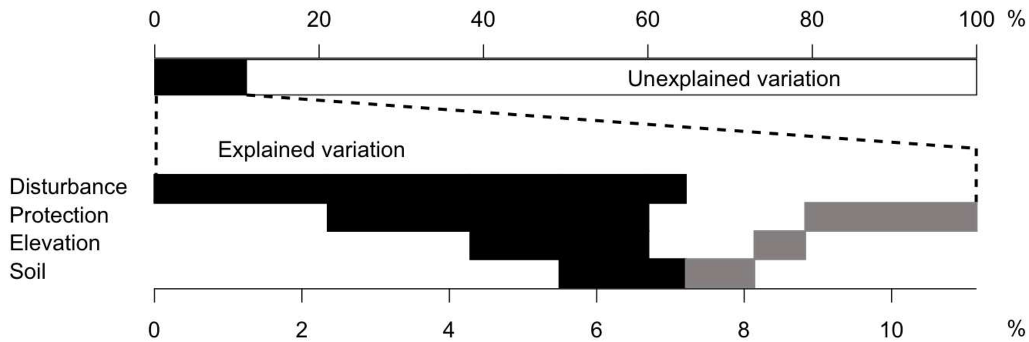

FIGURE 7: Variation partitioning based on partial RDA again highlights a strong collinearity between protection, elevation and the disturbance regime in explaining species composition. However, the contribution of elevation, protection and soil (moisture, pH, organic carbon, P, N, Mg) independent from disturbance (shaded in grey) sums up to more than a third of the explained variation.

Similarity values were within equal ranges in Satchari National Park, Satchari Reserved Forest and the surrounding area when species composition was compared between all plots of the subsample (see Fig. 8a). Plots in Satchari Reserved Forest showed the lowest values for plot “uniqueness” (Fig. 8b). These plots were more similar to all other plots in the data set than those of the National Park and the Surrounding Area. Similarity in species composition (Sørensen) decreased significantly with distance (“distance-decay”) but provided a poor fit (r^2 = 0.026***).

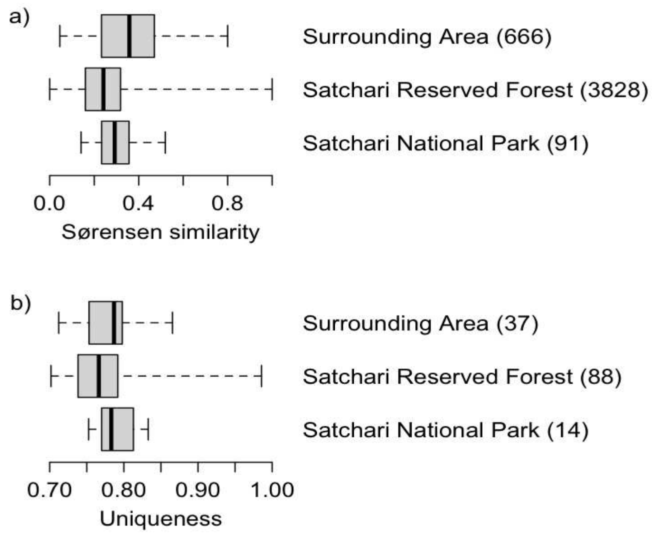

FIGURE 8: (A) Similarity in species composition calculated by comparing all plots within a subset. Values are smaller for Satchari Reserved Forest compared to both: Surrounding and National Park (B) Plot "uniqueness"(a focal plot compared to all other plots in the data set) reveals roughly the same pattern. Dark lines in the box-and-whisker plots represent the median; boxes indicate quartiles and whiskers data extremes.

DISCUSSION

SPECIES RICHNESS—Environmental variables and protection status equally contribute to the explanation of plant species richness patterns. However, the major gradient is in strong collinearity with the disturbance regime that has the largest explanatory power. Environmental variables are dominated by elevation. Soil conditions only contribute to a minor part for the explanation of species richness patterns. They seem to be more important for species composition. Evidence from other studies also suggests that species richness in tropical forests is largely independent from soil quality (Clinebell *et al.* 1995, Hill *et al.* 2005). Moisture content, that we found to be the only soil variable that is significantly related to the species richness pattern, is known for its temporal variability and strong dependence on precipitation events. Sampling was affected during the dry periods in winter and pre-monsoon and thus reflects the period where water shortage may show a spatial pattern.

Disturbance intensity (mainly human induced) is increasing towards low altitude less protected areas. This indicates a strong gradient of anthropogenic influence leaving the high elevation, high protected sites most pristine. This pattern is consisted with finding in Bangladesh (Islam *et al.* 2001) and Southeast Asia were anthropogenic disturbances strongly alter ecological health (Sodhi *et al.* 2009).

The identified explanatory power of topographic variables (even after correction for disturbances) is rather surprising given an elevation gradient of only 70 m of relative altitudinal differences. Microclimate and water supply (connected to topography) are probably more important than the elevational gradient itself. The influence of elevation might also be explained by current and subrecent erosion. However, slope did not reveal major influence, while one would assume that steeper slopes trigger land slides and erosion. Low elevation areas are more exposed to flooding or have closer connection to aquifers and water supply. Even if the correlation between elevation and soil moisture is low ($r^2 = 0.05$**), the tree roots may have access to the surface-near groundwater that is not reflected in soil conditions.

Protected areas were found to be most important for local species richness as well as for conserving the nature and natural resources (Lewis 2006) and especially plantations are identified to be depauperated in terms of species richness (Shukla 2009). This coincided with our findings that the protected portion of the study area has the highest average alpha-diversity. The strong collinearity with the disturbance regime indicates the importance and effectiveness of nature protection to protect species rich sites from overexploitation. This demonstrates that nature protection plays a crucial role for the preservation of species richness in the study area and that the efforts of keeping illegal land use from the protected areas have to be intensified.

The decision where to establish Satchari National Park might have been influenced by environmental circumstances. It is likely that the protected area was established covering the last remnant patches of high biodiversity forests. Wet spots as well as difficult to access higher elevations are less favourable for agriculture. Roughly half of the variation in species richness is explained jointly by environmental variables and land use regime (namely protection status). Anthropogenic use is decreasing with elevation resulting in highest human disturbances in low elevation areas. Whether this has also been the case in the pre protection time is unclear and the question of circular reasoning and autocorrelation has jet to be solved.

Today, Satchari Protected Area (not so much the National Park core area) is under constant pressure from human clearings and illegal impacts. Given the high population density and rise in Bangladesh combined with an increasing stress on agriculture by climate change, land use pressure on protected areas will increase.

SIMILARITY IN SPECIES COMPOSITION—Similarity in species composition is one of the central concepts of beta-diversity. It is a fundamental tool to describe the spatial pattern of biodiversity (Koleff *et al.* 2003). However, a variety of different concepts for beta-diversity exists (Tuomisto 2010 a,b) and a generally accepted concept is still missing. Jurasinski *et al.* (2009) suggest the term ‘‘differentiation diversity’’ for all cases where compositional similarity is addressed.

In our study, the pattern of similarity in species composition can be attributed to two major gradients (Fig .6a). The strongest gradient is dominated by the disturbance regime in collinearity with protection status along an altitudinal gradient. The study area thus seems to be characterized by less protected, high disturbed lowland areas and highly protected less disturbed high elevation areas. If the historic decision, where to place the national park, has been based on comparable biotic patterns, it might result from water availability for the water demanding agriculture that is less favored in higher sites.

The second gradient in species composition is strongly linked to soil characteristics (e.g. pH, Mg, organic carbon, N, P), a pattern that was not found for species richness. If the disturbance gradient is corrected for (Fig 6b, Fig. 7), a slight collinearity with elevation indicates that the gradient in soil characteristics is also an elevation gradient. The influence in disturbances on species composition is less pronounced than on the species richness pattern.

On a larger regional scale, disturbances are besides rainfall often reported to influence species composition (Ramesh *et al.* 2010). Differences in environmental and edaphic characteristics are often suspected to have a major influence on these scales but this hypothesis is rarely tested (Ramesh *et al.* 2010). Our analyses indicate that this hypothesis is valid.

Similarity is changing along spatial gradients. In Satchari the linear regression of decline in species composition similarity with distance ("distance-decay") is consistent with other small scale studies of distance-decay in tropical (Palmer & Maurer 2005, Jones *et al.* 2006) and temperate ecosystems (Girdler & Barrie 2008). The decline in similarity along the elevation gradient is not surprising but remarkably steep for the slight differences. The vertical difference is too small (70 m) for considerable temperature gradients. The fact that the first DCA axis is significantly related to protection status as well as to elevation, however, indicates a strong human influence on species composition in the study area and that human impact is correlated with topography.

A comparable pattern for similarity (plots compared within the subsets, Fig. 8a) and uniqueness (plot compared to all other plots, Fig. 8b) is counterintuitive as one would expect similar plots to be less unique. Land use may also serve as an explanation for this pattern. Both, the highly protected core area of Satchari National Park as well as the intensely used surrounding areas are characterised by a homogeneous disturbance regime. Satchari National Park is not exposed to agroforestry but dominated on the whole area by natural disturbances, while the surrounding areas are exposed to land use (tea plantations). Mainly those species that are well adapted to specific disturbance regimes will be supported in both areas. In consequence, the similarity within these subsets is high. This is in contrast to Satchari Reserved Forest, where a patchy and heterogeneous land use regime that is characterised by occasional (illegal) human impacts (clearings, plantations etc.) provides conditions for plant species that are either adapted to human management or natural disturbance regimes. Because the human influence is spatially (and probably temporally) heterogeneous, the plots within Satchari Reserved Forest are different in terms of site conditions for plants. Similarity in species composition is therefore low. However, sensitive species that are specialised either to a strictly natural or anthropogenic system will not grow in Satchari Reserved Forest. Plot uniqueness is thus higher in the National Park and in the surrounding areas.

This shows that modest human impacts may enhance the spatial heterogeneity of protected areas and thus create a higher diversity of spatial and ecological niches. Nevertheless, this increase in heterogeneity may interfere with the goals of preserving target species that might respond sensitively to disturbances (e.g. mammals). Species well adapted to human use are often cosmopolitans.

CONCLUSIONS—Bangladesh is one of the countries with the highest population density in the world. Still ongoing population growth and increasing land use pressure is the most serious problem for the country. In addition, changes in temperature and weather extremes (flooding) as well as the projected sea level rise could dramatically affect the countries densely populated areas and will thus further increase population pressure on forested ecosystems.

As a tropical country, Bangladesh is hosting a high diversity of organisms and remnants of long-term established ecosystems. Only very few remnants of this type of ecosystems are left over.

The results of this paper indicate that the future impact of human activities on biodiversity in Bangladesh forest ecosystems is essential for the protection of species richness and composition. However, protection strategies can not ignore the local population and have to incorporate livelihood and development (Chazdon *et al.* 2009, Chowdhury & Koike 2010a). Therefore, the increasing anthropogenic pressure urges to provide alternative ways of income for local people. Sustainable strategies are aiming towards win-win situations for man and biosphere (Chowdhury & Koike 2010b). In Bangladesh, locally based, participatory forestry is of special importance as institutional enforcement of sustainable forestry is still facing severe challenges (Muhammed *et al.* 2008). However, institutional work has significantly improved since the forest policy formulated in 1994. Sustainably used forest is different from pristine, but represent the natural response of forests to the new environmental conditions created by human activity (Lugo 2009). These sustainably used forests must be strictly managed to prevent a depletion of natural diversity (Tabarelli 2010). They are by no means an alternative to strictly protected areas without human interference. These areas are essential to protect species adapted to the natural environmental disturbance system.

In the Satchari National Park the elevated and also the wet sites are hosting the highest species diversity. These areas have not been suitable for agriculture in the past, but growing human pressure will increasingly endanger these specific ecosystems and the habitats of rare species. Here, the exclusion of any human interference has to be strengthened. But generally, both, the complete protection as well as the design of areas with sustainable use of forest biodiversity can be seen as equally important goals for a framework of biodiversity conservation in the few protected as well as in the other forested areas of Bangladesh.

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Stand Characteristics and Spatial Species Aggregation in a Bangladesh Forest Ecosystem

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Abstract: Assessing the spatial structures of forest ecosystems is important for forestry and nature conservation. However, only few studies deal with two-dimensional spatial heterogeneity of tropical forests. We determined the stand characteristics and spatial patterns in a tropical forest in Bangladesh. We focused on trees, as they are the most conspicuous components. We recorded tree species composition, in a systematic plot design, measured diameter at breast height for each individual tree, and calculated decay in similarity of tree species composition with geographical distance. The distance-decay was assessed separately for the whole study area and for two subsamples from Satchari National Park and Satchari Reserve Forest. Biomass increased significantly with protection status although tree individuals were smaller in the National Park. Plots in the Reserve Forest were associated with higher species turnover than in the National Park. We conclude that spatial decay in similarity of species composition is increasing with anthropogenic disturbances.

Keywords: diameter at breast height; beta diversity; distance-decay; national park; reserve forest; management; conservation

1. Introduction

The emergence of characteristic spatial patterns of biotic information is a common phenomenon in ecosystems. Detecting such patterns gives support to hypotheses on functioning and diversity. Besides alpha diversity, beta diversity can be applied to a spatial context in order to identify spatial heterogeneity. The decrease of similarity between any two observations with distance is referred to as the "first law of geography" [1]. In ecology, it is mostly applied to species composition [2-5]. It serves as a novel perspective to analyse spatial patterns of turnover in biodiversity [6-8].

A way to quantify the decrease of similarity between records are distance-decay curves, which are a function of similarity between biotic entities and their spatial distance. Such curves have been applied for a wide range of organisms, geographic gradients, environments (climatic gradients) and ecosystems or communities [6,9-11]. However, little is known until now about spatial patterns in species rich tropical forest ecosystems. In addition, rapid and unbiased methods are needed for biodiversity assessments especially in the tropics in order to document and analyse potential changes of biodiversity.

A decline of similarity in species composition can result from various reasons such as environmental heterogeneity [9,12,13], dispersal limitation [9,14,15], abiotic and biotic disturbances [10,16], and non-stochastic organismic (animal) behaviour [17-19]. It can be also an expected outcome of the balance between speciation and stochastic loss of species in landscapes [6,20,21]. However, Nekola & White [2], who pioneered formal and quantitative analyses of distance-decay in plant communities, highlighted the two following causes: a) the decay of environmental similarity with distance (e.g. climatic gradients), which renders the ability of organisms to adapt to environmental changes; b) the dispersal limitation due to ecological barriers and filters, which restricts the exchange of biotic information in space (seed transport, migration etc.).

Trees are the major structural components of forest ecosystems. They are supporting total species diversity and ecosystem fluxes and functioning (e.g.

microclimate, nutrient availability). In tropical forests, tree species diversity is extraordinarily high [22] and important for a whole legacy of other species. Thus, it is essential to consider the distribution patterns of trees; and to disentangle the effects of environment and distance on these patterns.

In this study, we characterise and examine stand structure as well as distance-decay of tree species in a nature reserve forest of Bangladesh. Stand characteristics are important for forestry. Planning and management rely on information on wood volume or tree biomass in particular forest stands [23,24]. However, these community traits are also of ecological importance. We calculate the decline in tree composition with geographic distance for the whole study area and then compare two areas of different protection status within Satchari Reserved Forest located in north-eastern Bangladesh. We choose both, a similar plot size and area under study i.e. national park and reserve forest as the distance-decay analyses are highly sensitive to spatial grain and extent [25].

2. Methods

2.1. Study area

The study was conducted in forest ecosystems of Bangladesh, where knowledge about diversity patterns is scarce. We focused on Satchari forest, which can be divided into three parts of different protection status: 1) Satchari National Park, 2) Satchari Reserved Forest, and 3) Surrounding Areas (dominated with tea gardens and fallow lands). The study area is located in north-eastern Bangladesh and stretches between approximately N$24^0 5''$ and $24^0 9''$ and E$91^0 24''$ and $92^0 29''$. It covers an area of approximately 40 km^2.

The study area is characterized by sandy loam to silt clay acidic soils and gently undulating to hilly topography (10 to 105 m a.s.l.). The climate is sub-tropical and monsoonic. The rainy season usually extends from June to September; however, the rainfall is irregularly distributed and erratic. Mean annual rainfall is 4162 mm. Most of the rainfall is received during the monsoon season. The relative humidity ranges from 74% during December to 90% during July to August. The mean minimum and mean maximum temperatures during January and May are 12 ^{0}C and 32 ^{0}C, respectively [26].

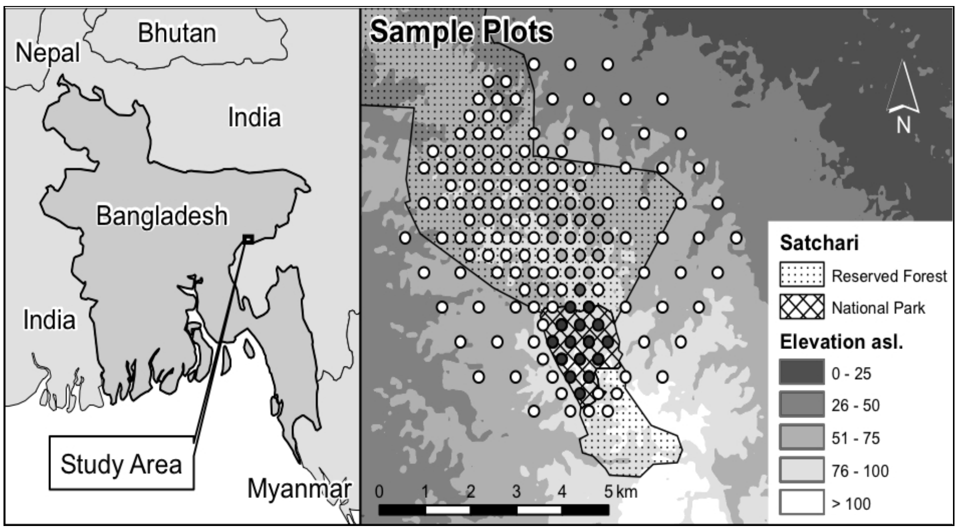
The natural vegetation of the study area consists of a mixed tropical evergreen forest. This type is mostly restricted to Satchari National Park. While human disturbances are excluded from Satchari National Park, other forests are subjected to different (legal and illegal) usage. The area is characterized by a well-developed tree stratum with evergreen top canopy trees. Almost all of the adjoining areas of the forest are covered by tea gardens. Research on Satchari Reserved Forest is sparse and concentrates on management and conservation of rural livelihoods and wildlife [27-29].

2.2. Sampling design

The study is based on an assessment of tree species characteristics and composition through the sampling of three protection units: 1) Satchari National Park, 2) Satchari Reserved Forest, and 3) Surrounding Areas. A representative, unbiased and systematic sampling procedure was applied for the whole study area. Our approach can be applied within a short time frame and is appropriate for rapid assessments and thus for temporal comparison during the following years. An equidistant sampling grid (distance of 400m for national park and reserved forest and 800m for surrounding areas) was implemented in the selected study area (Figure 1).

In the surrounding areas of the protected reserves and the national park a less dense sampling distance was applied. According to biometric characteristics for all tree specimens in the plots, we measured diameter at breast height (DBH) at 1.3 m height from the ground, which is recognized as a standard and most widely used reference diameter for expressing tree or stand characteristics [24]. In our investigation, a “tree” is regarded as a woody plant with a minimum DBH of 10 cm. DBH was recorded within each circular plot of 10 m radius. For some species that could not be identified directly in the field, pressed samples were taken to the National Herbarium at National Botanical Garden, Dhaka University and Jahangirnagar University, for identification and confirmation. The nomenclature of families and genera follows the Encyclopedia of Flora and Fauna of Bangladesh [30]. The four botanical collections, which could not be identified to species or genus level, due to the lack of diagnostic features, were not included in our floristic analyses.

Figure 1. The study area in east Bangladesh covers the core area of Satchari National Park (shaded), the Satchari Reserved Forest (dotted area) as well as surrounding area outside the park where land use is dominated by tea plantations and settlements. Tree species frequency and diameter at breast height were measured in 159 systematically arranged plots (circles, oversized). Two sub samples from Satchari National Park (black circles) and Satchari Reserved Forest (grey circles) were compared in the distance-decay analysis (Figure adapted from Uddin et al. subm.).



2.3. Data analysis

Stand characteristics such as tree density, species number, and DBH were compared between the areas of different protection status using t-Test. The distance-decay relation was assessed for the whole study area as well as for two equal sized sub samples from Satchari National Park and Satchari Reserved Forest (Figure 1). The distance-decay relation was calculated by a linear regression (least squared with R^2 as the goodness-of-fit measure) between geographical distance and similarity in species composition. Mantel test with 1000 permutations was used to assess significance [31]. Floristic similarities in tree species composition were calculated for all possible pairs of plots using the Bray-Curtis Index that allows considering quantitative information for single species. Hence, species frequency within the plots is incorporated in the calculated values for this index. Three plots were excluded from the DBH calculations (t-tests) as they contained trees with extensive buttress roots which rendered the assessment of comparable DBH impossible. The statistical software used was R 2.10.0. [32] with the packages *vegan* version 1.17-0 [33] and *ecodist* [34].

3. Results

Within the area surveyed, we recorded 2207 tree individuals in 156 plots. 121 tree species were identified in this rather small area. *Artocarpus chaplasha* was the most frequent species, which was recorded with 201 individuals. It was followed by *Tectona grandis* (196 individuals), *Acacia auriculiformis* (193 individuals) and *Eucalyptus camaldulensis* (119). The three most species-rich genera were *Ficus* (ten species), *Albizia* (six species), and *Syzygium* (four species).

The number of tree individuals, tree species and cumulative DBH varies significantly between the protection classes (Figure 2 and Figure 3). Values for tree species diversity and abundance tend to increase significantly with protection status. Mean DBH, however, is significantly larger in the surrounding area compared to the National Park (p= 0.03). This is due to the fact that there forest cover is less dense and individual trees of economic interest can reach larger size. In addition, the reserved areas are rather young and human impact cannot be totally excluded during the last decades, which may also explain this result.

Figure 2: a) Tree species richness and b) tree basal area show a spatial pattern in the study area.

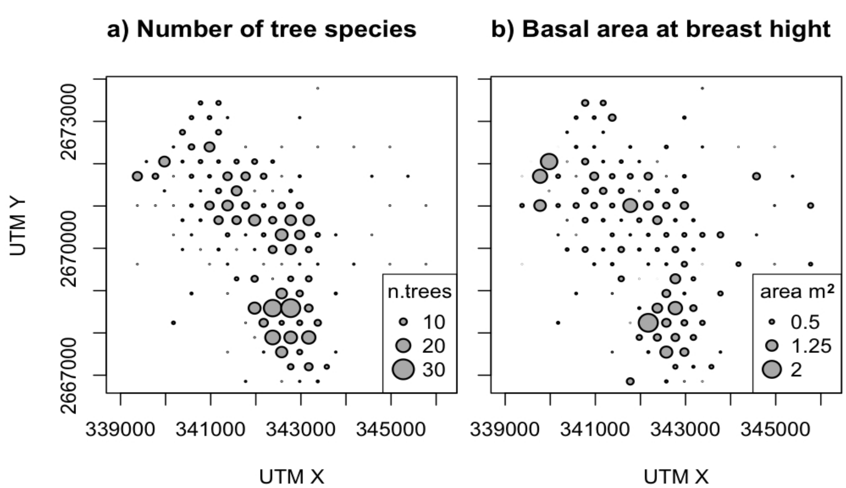
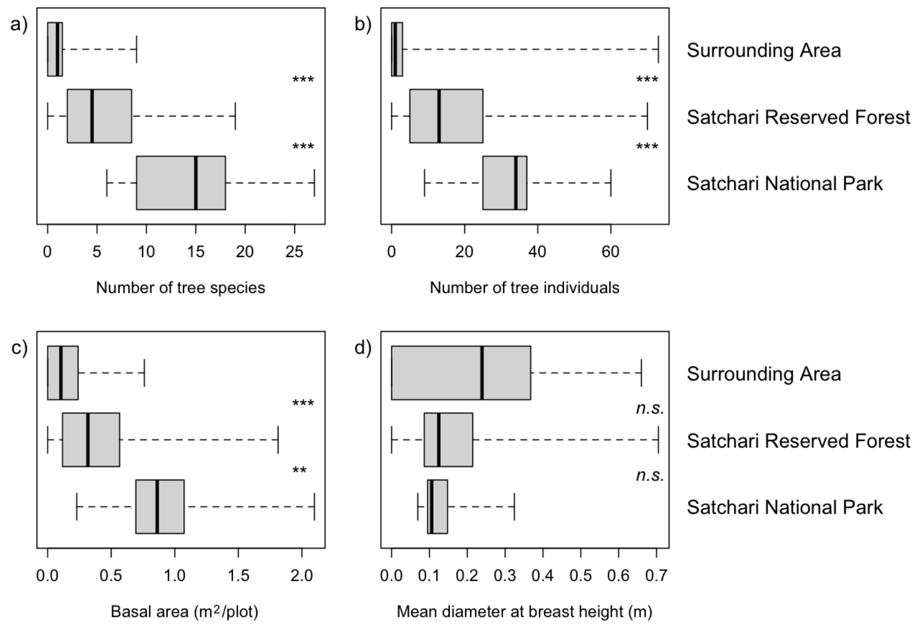


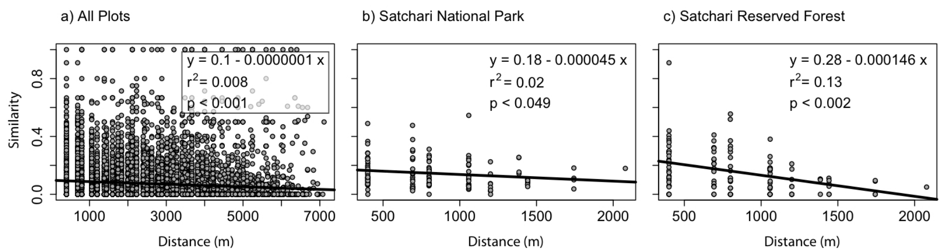
Figure 3. The number of tree species (a), tree individuals (b), and basal area (c) increases with protection status (significance between neighbors is indicated by stars: p<0.001***; p<0.01**). The mean DBH is highest outside of the reserved forest. However, only the comparison with the national park yields significant results (p= 0.03).



Tree species similarity was negatively correlated with geographic distances in general but the trend is not too clear (R^2: 0.008***; Figure 4a). However, the noise in these data is to be expected because of the consideration of all possible comparisons. In such a small area, spatial distance can be seen to be less important for the explanation of similarity between communities than land use or management impacts. Nevertheless, there is a spatial trend in our data set and investigation area.

However, the distance-decay patterns varied for the two sub-sampled protection classes (Figure 4b and Figure 4c). The decline in similarity of species composition with distance indicated by reserved forest (R^2: 0.13**; Figure 4c) was much steeper than that of the national park (R^2: 0.02*; Figure 4b). The communities of the national park area perform a higher similarity compared to the communities of the neighbouring reserved forest. This implies that the higher protection status obviously results in a more uniform and perhaps stable ecosystem.

Figure 4. a) Decline in similarity of species composition with distance in the whole study area. If the National Park and the Reserve Forest are considered separately, the slope of the distance-decay relationship is less steep in the National park (b) compared to the Reserved Forest (c).



4. Discussion

This case study proves that the effect of protected areas on biodiversity and spatial heterogeneity can be detected in tropical forests ecosystems on very fine spatial scales. Such kind of information is urgently needed in order to evaluate nature reserves at the regional and landscape. Even more important - especially for species rich tropical countries - the fulfilment of the targets of the CBD has to be proven by case studies that are time efficient and not costly. Our approach offers one option to implement spatially explicit biodiversity assessments that are independent from preferential observer bias. Our study is the first to explicitly investigate spatial patterns of tropical tree species composition in forest ecosystems of Bangladesh.

In this forest area, the mean number of tree species and of tree individuals at the plot level is increasing with protection status. However, simple quantitative biotic measurements result in a more differentiated image. Basal area, which indicates the total woody biomass (the surface that is covered by the stems), tends to increase with the protection status, which hints at a lower influence of exploitation and resource use. However, mean DBH was found to be larger in the surrounding areas. This may be surprising as trees may take less time to reach a certain DBH in undisturbed areas compared to disturbed areas [35]. Looking at the specific conditions on this area it becomes clear that the well-managed tree gardens and plantations that are located areas around the nature reserves exhibit single trees of large sizes that are well protected there. Illegal exploitation is almost impossible. In addition smaller trees and especially juveniles are systematically removed in order to support the cultivation of tea in the understory and between the shade trees.

Surprisingly, we detected spatial trends of community similarity in this rather small area. Distance-decay effects were reported for other tropical systems, but evidence is rare [36-38]. In the study area the slope of the distance-decay relation was found to be comparable to other studies of equal scale in tropical ecosystems [39,40]. However, this evidence is not sufficient to support the explanation general characteristics of ecosystem heterogeneity. Comparisons are restricted by differences in individual plot size and sampling density [41-43]. Nevertheless, we hypothesize that studies that are based on a proper systematic sampling design might result in comparable findings for the spatial traits of beta diversity and species turnover [44].

The stronger decline of similarity with distance within the Reserve Forest compared to the National Park was unexpected. The reasons for less distance-decay as well as higher species diversity in the National Park [45] can be related to niche saturation in the better protected and presumably more mature National Park ecosystems. However, this area is also differentiated from the others by elevation (and accessibility). In contrast to the National Park, the Reserve Forest exhibits a patchy mosaic of natural but also disturbed sites. The Reserve is protected by law but evidence for illegal exploitation was found during fieldwork. While on undisturbed sites, climax species have the option to become dominant, pioneer trees will preferentially grow on disturbed sites. This spatially fine-grained variation in disturbance regimes, which is missing in the National Park area, explains the decline in species similarity with distance in the Reserve Forest.

In tropical forests distance-decay may be explained by both, environmental filtering and neutrality [6]. Recent studies have emphasized that these processes are supplementary rather than mutually exclusive. Combined effect on floristic composition were documented [11,13,38,46-48]. The coupled effect of these mechanisms can be expected to be also influential for the distance-decay relationships in the Bangladesh forest ecosystems under investigation in this study.

In addition to spatial effects and disturbance regimes, other environmental site conditions are modifying spatial patterns of distance-decay. In our study, the environment can be regarded to be rather comparable in the whole study area. However, this aspect has to be considered when more structured landscapes and larger areas are investigated. Some studies found that environmental conditions were stronger predictors for floristic similarity than geographical distances [39,49]. Furthermore, complex tropical ecosystems can hardly be completely understood by abiotic and geographic parameters only. A large portion of the variation in species similarity in tropical forests remains unexplained [46].

Other factors, such as variation in species functional groups and differences in niche width among taxa might cause the distance-decay of similarity [2,38]. The seeds of many tree species in the tropics are dispersed by vertebrates such as birds or primates [50]. This directed dispersal can result in characteristic population patterns. Especially for the canopy trees, wind is also an important dispersal vector [51] and thus may result in spatial distribution patterns that are reflecting the exposition to the major wind direction.

Anthropogenic disturbances may blur distance-decay relations resulting from natural ecological processes. According to La Sorte *et al.* [10,52], anthropogenic activities are responsible for the strongest distance-decay in non-native European urban floras. Like other forest ecosystems in Bangladesh, the biodiversity in the study area is facing a noticeable threat from anthropogenic disturbances, mainly exploitation [53, 54].

In summary, the results of our study suggest that the similarity in tree species composition tends to decay very slightly with increasing distance in natural and protected tropical forests. However, the rate of spatial decay is strongly associated with anthropogenic disturbances, which are enhancing spatial heterogeneity.

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List of Publications*

*Publications listed from 1-4 were part of this thesis

Publications-Refereed Journal Articles

1. Mohammad Belal Uddin, Juergen Kreyling, Manuel J. Steinbauer & Carl Beierkuhnlein, in prep. Neglected or Negligible? Biological Invasions in Tropical Forests- ***Biological Invasions.***
2. Mohammad Belal Uddin, Manuel J. Steinbauer, Anke Jentsch & Carl Beierkuhnlein, resubmitted. Exotic Plant Species in Bangladesh Forest Ecosystems. ***Biological Invasions.***
3. Mohammad Belal Uddin, Manuel J. Steinbauer, Anke Jentsch & Carl Beierkuhnlein, resubmitted. The Influence of Habitat Characteristics and Nature Conservation on Biodiversity in a Bangladesh Forest Ecosystem. ***Biotropica.***
4. Mohammad Belal Uddin, Manuel J. Steinbauer & Carl Beierkuhnlein, submitted. Stand Characteristics and Spatial Species Aggregations in a Bangladesh Forest Ecosystem. ***Diversity.***
5. Mukul, Sharif Ahmed, **Uddin, Mohammad Belal**, Manzoor Rashid, A.Z.M. and Fox, Jefferson. 2010. 'Integrating livelihoods and conservation in protected areas: understanding the role and stakeholder views on prospects for non-timber forest products, a Bangladesh case study'. International Journal of Sustainable Development & World Ecology 17(2): 180 — 188.
6. **Uddin, M. B.**, Mukul, S.A. Khan M.A.S.A. and Hossain, M.K. 2009. Seedling responses of three agroforestry tree species to Phosphorous fertilizer application in Bangladesh**.** Journal of Forestry Research 20 (1): 45-48
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Publications-Abstracts Volume

1. **M.B. Uddin,** M.J. Steinbauer, C. Beierkuhnlein 2011. Distance decay patterns across anthropogenic landscape in Bangladesh-implications for biodiversity conservation. Abstract Volume. The 8th IALE World Congress: Landscape Ecology for Sustainable Environment and Culture to be held on 18-23 August, 2011 in Beijing, China. (Accepted with grant)

2. **M.B. Uddin,** M.J. Steinbauer, C. Beierkuhnlein 2011. The role of conservation patterns of habitat types on plant species diversity of a tropical forest in Bangladesh. Abstract Volume. Student Conference on Conservation Science (SCCS-Cambridge) held on 22-24 March, 2011 at the Department of Zoology, University of Cambridge, United Kingdom.

3. **M.B. Uddin** 2010. Livelihoods on Wetland Resources-A Case Study from Wetland Ecosystem in Bangladesh. Abstract Volume. International Conference on Wetland Ecosystem Services: Biodiversity, Livelihoods and Sustainability held on 17-21 November, 2010 at Khon Kaen University, Thailand.

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Declaration/Erklärung

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(Mohammad Belal Uddin) 3. Mai, 2011