Human hydrographical changes interact with propagule predation behaviour in Sri Lankan mangrove forests

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ABSTRACT

For mangroves with almost no tidal influence and a subsequent mosaic vegetation structure we describe the relation between propagule predators and both vegetation structure and environmental factors on a vegetation assemblage or 'forest patch' level. We then report the interaction between natural propagule predation and human influence. In different forest patches dominated by *Avicennia officinalis*, *Excoecaria agallocha*, *Lumnitzera racemosa*, *Rhizophora apiculata* or *R. mucronata* or in open or mixed areas identified from aerial photographs, the predation on propagules of *A. officinalis*, *B. gymnorrhiza*, *R. apiculata* and *R. mucronata* was monitored in a total of 24 experimental plots (3 per forest patch). Relationships to environmental factors (topography, water level, rainfall and season) on the level of predation were investigated. The highest predation intensity by crabs was on *A. officinalis* propagules, and in *E. agallocha* forest patches. Predation by crabs, snails, insects and mammals was observed, and the significant differences in predation intensity across species and across forest patches were explained directly by propagule predator identity and abundance, and by the interaction between rainfall, water level and microtopography. We illustrated how hydrography changes alter the behaviour of propagule predators and play a role in the shaping of vegetation structure by reconstructing the lagoon water level of a site over a period of 50 years based on rainfall data. This time frame covered both a condition without and with human impacts, and past and present propagule predation settings were confronted with the simulated hydrology. The importance of spatial and temporal microhabitat variations in opening multiple successional pathways in vegetation dynamics is illustrated, and is highly relevant for ecosystems with unpredictable or short-lived (<20 years) patchy vegetation structures and microhabitats.

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1. Introduction

Mangrove forests in some areas of the world have been reported to be very dynamic over short time frames and to display major structural differences in vegetation in less than 20 years (for example Lebigre, 1999; Sherman et al., 2000; Dahdouh-Guebas et al., 2000, 2002a; Duke, 2001; Cohen and Lara, 2003; Fromard et al., 2004; Benfield et al., 2005; Giri et al., 2007; Giri and Muhlhausen, 2008), and certain mangroves have been found to be threatened by 'cryptic ecological degradation' (Dahdouh-Guebas et al., 2005a). This dyna-mism is often the result of immediate response to direct human influences (Rakotomavo and Fromard, 2010), but mangroves can also respond to indirect human influences after a lapse of time, such as the colonization of neglected coconut plantations (Dahdouh-Guebas et al., 2002a), human-influenced secondary succession (for example Kairo et al., 2002), or further natural interactions after a human impact has diminished or disappeared (for example Dahdouh-Guebas et al., 2004).

Zoned mangroves, or mangroves that display a considerable topographic slope between lower and upper intertidal areas, display a spatially particular pattern in the vegetation structure (Snedaker, 1982; Smith, 1992). This vegetation structure has been investigated in a linear way based on other gradient-dependent factors (for example Rabinowitz, 1978; Jiménez and Sauter, 1991; McKee, 1993; Matthijs et al., 1999; Satyanarayana et al., 2002, 2010). A model offering an explanation for the vegetation structure of mangroves based on propagule predation in relation to tree dominance (not necessarily linked to zonation), is known as the dominance-predation hypothesis

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proposed by Smith (1987a). This hypothesis was tested along the Australia North coast (McGuinness, 1997b; Clarke and Kerrigan, 2002), in Malaysia (Smith et al., 1989), in Kenya (Dahdouh-Guebas et al., 1997, 1998), in Belize (McKee, 1995), in Florida (Smith et al., 1989), in Panama (Smith et al., 1989; Sousa and Mitchell, 1999) and in the Federated States of Micronesia (Allen et al., 2003). Results of some of these studies were compatible with the dominance-predation hypothesis (Smith et al., 1989), whereas most other studies invalidated it (for example McKee, 1995; McGuinness, 1997b; Sousa and Mitchell, 1999; Clarke and Kerrigan, 2002). However, even in the latter case questions on the role played by crabs, the prime propagule predators in mangroves, in mangrove regeneration or in the shaping of the vegetation structure, were raised but remained unanswered (Smith et al., 1991; Siddiqi, 1995; Steele et al., 1999; Dahdouh-Guebas et al., 2000, 2002b).

As opposed to 'zoned mangroves' as a study object in the earlier studies previously mentioned, this paper does not focus on mangroves with a regular topographic slope between upper and lower intertidal areas, or a conspicuous gradient in vegetation. Instead we focus on an irregular micro-topographical surface with many pools and islands, and on a vegetation structure with dynamic assemblages that are distributed in a 'moving mosaic', or that at most can be regarded as semi-zonation (Dahdouh-Guebas et al., 2000). For our study sites we set out knowing from previous studies that a patchy vegetation structure is present (Dahdouh-Guebas et al., 2000; Verheyden et al., 2002; Dahdouh-Guebas and Koedam, 2002), and that the vegetation assemblages appear to be very dynamic on a decadal scale (Dahdouh-Guebas et al., 2000, 2002a). Our definition of 'vegetation structure' follows that of Dahdouh-Guebas and Koedam (2002), i.e. the stand extent, (spatial) structure and composition of the vegetation.

The present research on propagule predation behaviour is new with respect to the site's tidal settings (most existing studies focus on daily tidal inundation), vegetation structure (most existing studies focus on zoned mangrove vegetation), and geographical location (no such studies carried out on the Indian subcontinent). The objectives follow a deductive outline starting with a confirmatory and descriptive section, an environmental analysis section, and finally a simulative section. The objectives of the present paper are therefore, first, to confirm the phenomenon of propagule predation in the assemblages of the earlier mentioned mosaic mangroves, second, to explore the links between the observations on predation and environmental and vegetation structure data, in particular the link between the predation intensity, water level and rainfall, and third, to simulate how historical changes in these relationships may influence the vegetation structure of mangroves.

2. Material and methods

2.1. Description of the study sites

Two mangrove forests were investigated in Sri Lanka, along the South-Western side of the island, where the spring tidal amplitude is less than 1 m (Spalding et al., 1997), but locally rarely exceeds 15 cm in the course of one week (in <16% of the time it does exceed this figure; personal measurements 1997–1999).

The first mangrove forest is located between Galle and Unawatuna (06° 01′ N–80° 14′ E), in the wet climate zone of Sri Lanka (Mueller-Dombois, 1968) and had a mean annual rainfall of 2379 mm over the last 50 years. This basin and riverine mangrove type (*sensu* Lugo and Snedaker, 1974) covers an area of 1.5 km² and is located at about 600 m from the Indian Ocean shore (Fig. 1). Two rivers run through the mangrove forest, namely the Thalpe Ela, discharging into the ocean, and the Galu Ganga, a tributary of the former. The study concentrates on the centrally located area that is known to display a high degree of dynamism. The vegetation structure of mangroves in

Galle has been investigated in detail by Dahdouh-Guebas et al. (2000), Verheyden et al. (2002), and De Smet (2005) and comprises three distinct patches (a vegetation 'patch' is here defined as a polygon with no determined shape or area and having a certain, often monospecific, floristic composition): one dominated by *Excoecaria agallocha* L., one dominated by *Rhizophora apiculata* Bl. (hereafter referred to as the patch dominated by *Rhizophora* spp. to allow comparison with the second mangrove site; see later) and an 'Open Space' in which the herb layer is dominated by *Fimbristylis salbundia* (Nees) Kunth subsp. *pentaptera* (Nees) T. Koyama. 'Dominance' is defined with respect to the canopy and therefore detectable on remote sensing imagery, and is also reflected in the importance value of species (see Dahdouh-Guebas et al., 2000). The mangrove forest in Galle has been subjected to human influence over the last 50 years (Dahdouh-Guebas et al., 2000; Mulder, 2005), the major one of which was the construction of a dam (Fig. 1D and F) on the Galu Ganga near its point of discharge into the Thalpe Ela and the construction of a 1 km raised path through the mangrove forest, which starts at the dam and is slightly inclined down in the second half of its track (Fig. 1D and E). This path is also a construction all along the banks of the Galu Ganga (Fig. 1C).

The second mangrove forest is in the Pambala area of Chilaw Lagoon, located in Sri Lanka's intermediate climate zone (Mueller-Dombois, 1968), and had a mean annual rainfall of 1443 mm over the last 50 years. The mangroves here are of the fringe type (*sensu* Lugo and Snedaker, 1974), and have a rather irregular distribution along a complex of creeks (Marambettiya Ela, Bate Ela, Pol Ela and Dutch Channel). Most freshwater influx stems from the Karambalan Oya catchment, whereas outflow to the sea is possible at the townships of Chilaw (07° 35′48″ N, 079° 47′ 25″ E) and Toduwawa (07° 29′30″ N, 079° 48′ 16″ E). This site is known to be the most species-rich in South-Western Sri Lanka (Jayatissa et al., 2002). The vegetation structure of this mangrove forest has been studied in detail by Zetterström (1998), Verheyden et al. (2002), and De Smet (2005), and comprises five distinct patches: one dominated by *Avicennia officinalis* L., one dominated by *E. agallocha*, one dominated by *Lumnitzera racemosa* Willd., one dominated by *Rhizophora mucronata* Lam. and *R. apiculata* (hereafter referred to as the patch dominated by *Rhizophora* spp.), and a 'mixed' patch comprising *E. agallocha, L. racemosa, Heritiera littoralis* Dryand. and *Xylocarpus granatum* Koen. Other common species in Pambala, although never dominant or co-dominant, are *Bruguiera gymnorrhiza* (L.) Lam. and *B. sexangula* (Lour.) Poir. Occasionally *Aegiceras corniculatum* (L.) Blanco was observed. To a small extent some of the patches in Pambala could be regarded as constituting a semi-zonation (a vegetation 'zone' is defined as a band-like patch of vegetation with a certain, often monospecific floristic composition). The mangroves in Chilaw Lagoon have recently been subjected to strong human influences such as clearing and pollution as a result of shrimp farming (Foell et al., 1999; Dahdouh-Guebas et al., 2002c).

In both mangrove forests there was no slope with upper or lower intertidal areas, but rather a plateau with water pools, many in Galle and few in Pambala. The forest patches were contiguous allowing natural dispersal of propagules across their boundaries. In both mangrove forests the study focused on those areas that had been investigated before with respect to their vegetation structure and past vegetation structure dynamics. It concentrated on the central vegetation patches that were representative to conduct the predation experiments. Because of the limitation of most forest patches to a single large one per dominant species, and because forest patches similar in species composition in farther back-mangrove areas had very different environmental settings, consistent replication between forest patches within a site was not possible. However, remote sensing and ground truth analysis was used to reflect the homogeneity of the small and large patches, as well as their representativeness (see Dahdouh-Guebas et al., 2000; Verheyden et al., 2002; De Smet, 2005). Mangrove nomenclature follows Tomlinson (1986).
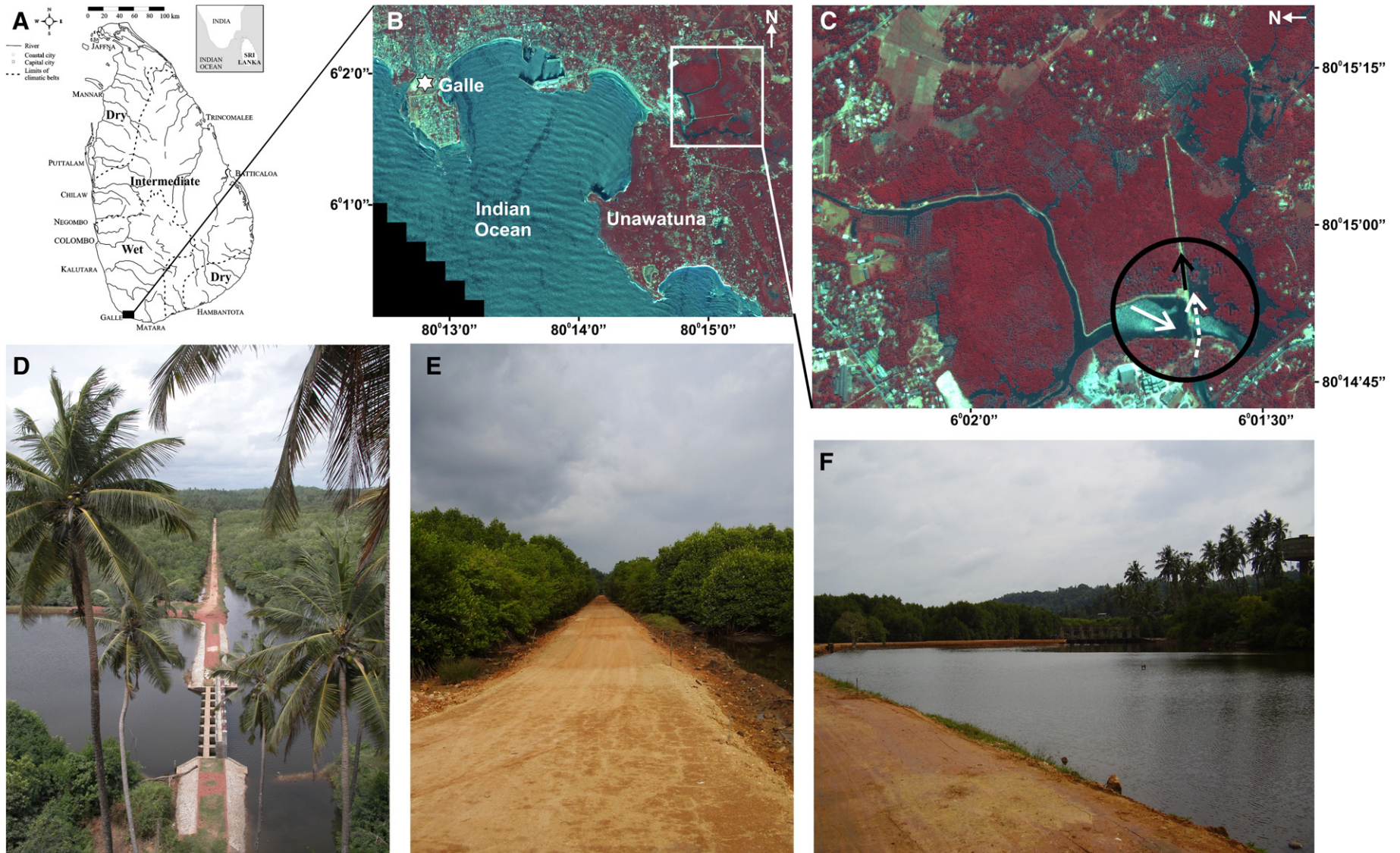
Fig. 1. (A) Map of Sri Lanka indicating the Galle-Unawatuna area. (B) Quickbird satellite imagery of the Galle-Unawatuna area. (C) Mangrove forest under study with a magnifying lens over the dam. Within the lens the long black arrow shows from where and in which direction the photograph in D was taken, whereas the short black and white arrows show the same for the photographs in E and F. (D) View from the water tower of a nearby cement company showing the mangrove forest with the raised path along the bank of the Galu Ganga (partly hidden by the two coconut trees on the left), and the dam on the foreground (between the coconut trees). (E) View of one of the creeks and of the dam taken from the raised path. (F) View of the raised path. Note that this path is approximately 1 km long and it is inclined to the back of the photograph.

2.2. Propagule predation

This section deals with whether or not propagule predation is present and whether or not differential predation patterns exist between forest patches or between experimental propagule species. The bulk of our fieldwork consisted of the propagule predation experiments detailed later, but we also collected information on propagule predation by visual observation.

After exploratory experiments done in Galle in March 1998 (dry season), the main fieldwork in Galle and Pambala was conducted from October until December 1999 (wet season). The experiments were done with propagules from viviparous mangrove species tethered to plants or immobile debris in experimental predation plots and within different forest patches as indicated in Table 1. Shorter tethers leading to artefacts (McGuinness, 1997a), we used strong 1 m long nylon line for all propagules. Propagules were used in proportions (based on densities and frequencies) approximating the availability of propagules in the propagule-producing bulk of the forest at the time of propagule collection (rounded to the nearest multiple of ten) (Table 1). The rationale to use the propagule availability in a wider area of the forest was because the propagules are largely produced in these patches and they have the possibility to float from one forest patch to another. All propagules collected were mature and gathered fresh from the tree, but for *R. mucronata*. Propagules of the latter species were not available in sufficient quantities fresh, and were therefore collected from the mangrove floor and from natural ponds instead, provided they did not show signs of decay, damage, predation or rooting. During the exploratory experiments undertaken in Galle in 1998 only *B. gymnorrhiza* propagules were available and 20 were used per plot.

Every day (in Galle) or every other day (in Pambala), the plots were visited and the predation status was recorded for each of the propagules. Propagules were classified as 'predated' in any of the three cases defined by Smith (1987a, 1987b): when the epicotyl was eaten, when at least 50% of the hypocotyl was cut through or when the propagule was pulled into the burrow of a predator. If the hypocotyl was cut through for less than 50%, the propagule was classified as 'damaged', whereas in all other cases it was classified as 'intact'. In a few cases the propagule had disappeared and was recorded as 'lost'. The experiment was ended when all the propagules were eaten or when the frequency of propagules within each predation class had levelled off (*i.e.* after two weeks).

Two control experiments were established in order to check for the effect of freshness (because we collected *R. mucronata* freshly from the tree, see previous) and of predator damage on the growth performance. To evaluate the effect of propagule freshness, 44 *R. mucronata* propagules, 22 freshly gathered and 22 taken from the mangrove soil and water ponds, were planted vertically into the soil, and both the predation and development status (number and length of leaves and roots) were checked daily for two weeks. Using the same procedure, the effect of predator damage was investigated by assessing 14 undamaged and 13 damaged *R. apiculata* propagules planted. The rationale for these control experiments is to make sure that our assumptions are correct. The assumptions were (1) that the propagules collected from the mangrove floor and from ponds indeed had the same viability as those collected fresh, and (2) that damaged (*i.e.* not 'predated' *sensu* Smith, 1987a, 1987b) propagules still had the same viability as undamaged propagules.

2.3. Biotic and abiotic environmental factors

This section explores the relation between predation patterns and environmental factors and between predation patterns and dominant vegetation cover.

In each of the forest patches between 13 and 64 points (depending on the size of the patch, see Dahdouh-Guebas et al., 2000) were sampled for land/water ratio (visual estimation in 10 m × 10 m plots delimited by coconut wire), crab burrow density and density of the snail *Terebralia palustris* L. (in 1 m² plots). For the density of crab burrows, only burrows larger than 3 cm, and belonging to crabs likely to be propagule predators (mainly sesarmids), were considered after reconnaissance surveys on the crabs' behaviours. During these reconnaissance surveys also other propagule predators were observed. The earlier mentioned biotic factors were chosen as they have been shown to play a role in predation (Dahdouh-Guebas et al., 1997; McGuinness, 1997a, 1997b). In addition, we focused on the lagoon water level, as this factor has been suggested to play a role, without experimental data being available (Cannicci et al., 2008).

The water level (in cm) of the lagoon in Pambala was recorded daily from a fixed scale at the Mangrove Conservation and Demonstration Centre of the Small Fishers Federation of Lanka (SFFL). Analytical use of this date-dependent variable was done taking into account the different starting dates for the experiments in the different forest patches.

Information with respect to the past and present changes in the mangrove forest and with respect to adult, young and juvenile vegetation data (densities, frequencies, basal area, cover, etc.) were taken from studies done between 1997 and 1999 (Zetterström, 1998; Dahdouh-Guebas et al., 2000, 2002c; Verheyden et al., 2002) and used appropriate to visualise the link between propagule predation and the vegetation structure and its dynamics. The validity of the dominance-predation hypothesis (Smith, 1987a, 1987b) was tested for the species in the present study, but rather than only based on basal area, the dominance is reflected here by the importance value of Curtis (1959), which is based on measurements of density, frequency and basal area. These data were from Dahdouh-Guebas et al. (2000) and measured or calculated as described therein.

Although the toxic *E. agallocha* (Euphorbiaceae) is ubiquitous as a co-dominant species, its seeds or leaves were never observed to be consumed locally by propagule predators. In addition, this species has

Table 1

Experimental design for the fieldwork in 1999 in terms of sites, forest patches, experimental plots and propagules used. See text for the rationale of translating background propagule input into experimental numbers. The same proportions of propagules were used in all experimental plots.

# Forest patches	# Experimental plots of 5 × 5 m²	Natural background propagule input	# Experimental propagules
Galle			
1 *E. agallocha*[*]	3	45.3% *B. gymnorrhiza*	10 *B. gymnorrhiza*
1 Open space[*]	3	54.7% *R. apiculata*	10 *R. apiculata*
1 *Rhizophora* spp.[*]	3		
Pambala			
1 *A. officinalis*[*]	3	21.6% *A. officinalis*	10 *A. officinalis*
1 *E. agallocha*[*]	3	34.7% *B. gymnorrhiza*	10 *B. gymnorrhiza*
1 *L. racemosa*[*]	3	43.7% *Rhizophora* spp.	5 *R. apiculata*
1 mixed[*]	3		15 *R. mucronata*
1 *Rhizophora* spp.[*]	3		

[*]The only one representative (see text).

small seeds instead of propagules like the viviparous mangrove species, and was therefore not included in this study.

2.4. Simulating historical lagoon water level

This section focuses on lagoon water level as an influential environmental factor and links it to rainfall patterns in a historic perspective.

Rainfall data for Galle and Chilaw, available from the Meteorological Department in Colombo, were collected for the period 1948–1999. Water level for Galle was recorded daily from February 1997 until June 1999 at the landward side of the dam. With the knowledge of past changes in the mangroves in Galle involving the construction of a raised path and dam, the relationship between lagoon water level and rainfall was explored and the relationship between propagule predation and water level extrapolated to past conditions. Simulations of the hydrological conditions that influence propagule predation and prop-agule dispersion before and after the construction of road and dam infrastructure across the mangrove forest in Galle were compared. As the explanation of the procedure of the simulations is strongly interacting with the results, we prefer to fully report this aspect in the results section.

2.5. Statistical analyses

The χ^2-test and the G-test were used to test the significance of the differences in growth performance classes observed in the control experiments. Using GMAV5 for Windows, in-depth ANOVA analyses were performed on the arcsine transformed propagule predation intensities after 13 or 14 days of observation (days after which the predation intensity levelled off, see results Fig. 2) on each of the following levels:

i. within and between the different propagule 'species' and 'forest patches' in each site (two-way experimental design with a factor propagule 'species' and a factor 'forest patch');
ii. between the *E. agallocha* and the *Rhizophora* spp. forest patch of Galle and Pambala (three-way mixed experimental design with the factor 'forest patch' nested in the factor 'site' and the factor propagule 'species' as orthogonal);
iii. between the wet and the dry seasons (two-way experimental design only applicable to *B. gymnorrhiza* in Galle with a factor 'forest patch' and a factor 'season').

The Student-Newman–Keuls test (SNK test) was used to identify which factors were significantly different in the analyses of variance. Correlation and regression analyses were used to test the relationship between predation and lagoon water level.

3. Results

3.1. Propagule predation (observations on herbivores and propagule predators)

In both sites, the predominant grapsid crabs are *Neosarmatium malabaricum* (Henderson), *Episesarma tetragonum* (Fabricius) and *Perisesarma dussumieri* (A. Milne-Edwards), and to a lesser extent also *Neosarmatium meinerti* (De Man) where present. These species usually occur in places with a rather high elevation, such as the *E. agallocha* patches, or the *Rhizophora* spp. forest patch in Galle, where the topography is raised by the burrowing activities of the mangrove mud lobster *Thalassina anomala* Herbst. Other grapsid crabs observed are:

Pseudosesarma crassimanum (De Man), *Neosarmatium smithii* (H. Milne-Edwards), cf. *Metopograpsus thukuhar* (Owen), *Parasesarma plicatum* (Latreille), cf. *Parasesarma asperum* (Heller) and *Perisesarma* sp.nov. (Peter Davie, pers. comm., 2003). *Cardisoma carnifex* Herbst was observed in Galle along the elevated paths through the mangrove forest, and was observed predating on *B. gymnorrhiza* propagules artificially brought in their vicinity (Verheyden, 1997). However, this crab species was never recorded within the mangrove forest in Galle, where the vegetation dynamics take place, and propagules were never observed to strand in their vicinity naturally, and hence it was not investigated.

T. palustris is responsible for the greater part of predation on *B. gymnorrhiza* in the 'open space' and was never observed predating on *R. apiculata* propagules. Propagules predated by this gastropod had always the epicotyl scraped off first, whereas in a few cases the hypocotyl was affected only later or not at all. Crabs on the other hand, seldom affect the epicotyl and prefer to cut through the hypocotyl. Not only crabs and snails were observed predating on fallen propagules, but also rodents such as rats and squirrels, although it is not clear whether the latter only access fallen propagules or actually cause them to fall as well. It was however clear that propagules predated by crabs were most commonly found pulled within a burrow and consumed there, whereas propagules consumed by snails or by rodents were left on the mangrove soil in open air. This observation also removes another artefact discussed by McGuinness (1997a), which is that of crab predators being unable to pull the propagules into their burrow. Local people also reported the porcupine to consume mangrove propagules, and foot prints of these animals were found in the mangrove forest (pers. obs.). Finally, in Galle two yet unknown species of insects (a coleopteran and a dipteran) have been observed to destroy *B. gymnorrhiza* propagules by breeding, hatching and nursing inside the hypocotyl, while it is still attached to the parental tree. More than 70% of propagules were infested and we expect at least half that percentage not to survive because the hypocotyl was consumed or rotting from the inside (pers. obs.).

3.2. Differential predation patterns

The first control experiment did not show significant differences in predation effects between freshly gathered propagules and propa-gules taken from the mangrove soil and water ponds ($\chi^2 = 0.153$; d.f. = 1; n.s.) nor in growth performance of their leaves and roots (G = 10.561; d.f. = 6; n.s.). Similarly, there was no effect of predator damage in *R. apiculata* propagules, and the 'damaged' propagules were able to further develop roots and leaves like 'intact' propagules (G = 2.482; d.f. = 4; n.s.). Considering the absence of tidal effects or people in our plots, the 'lost' propagules were most probably removed by stronger animals such as rats or porcupines that were able to break the twine and take away the propagule. In addition not many propagules were 'damaged' or 'lost' (<4% and <10% respectively out of a total amount 780 experimental propagules). For the earlier mentioned reasons respectively, the classes 'intact' and 'damaged' and the classes 'predated' and 'lost' were combined during the statistical analysis to form two classes, one reflecting survival and one death. In Pambala, there were no significant differences between *R. mucronata* and *R. apiculata* propagules for data on predation ($\chi^2 = 0.243$; d.f. = 1; n.s.; after 13 days) so they were combined in the final analysis of predation rates and referred to as *Rhizophora* spp. propagules.

The predation intensity for each of the species and the forest patches in Galle and Pambala show that the curves are mostly asymptotic for all species in all forest patches (Fig. 2). Further ANOVA

Fig. 2. 1999 Predation intensity results for propagules of *B. gymnorrhiza* (A) and *Rhizophora* spp. (B) in Galle, and for propagules of *A. officinalis* (C), *B. gymnorrhiza* (D) and *Rhizophora* (E) in Pambala, in each of the respective forest patches abbreviated as follows: AO = *Avicennia officinalis*, EA = *Excoecaria agallocha*, LR = *Lumnitzera racemosa*, M = mixed mangrove, OS = open space, and R = *Rhizophora* spp. Every curve represents one forest patch. The asymptotic nature of the curves justifies further statistical analysis based on predation intensities after 14 days.
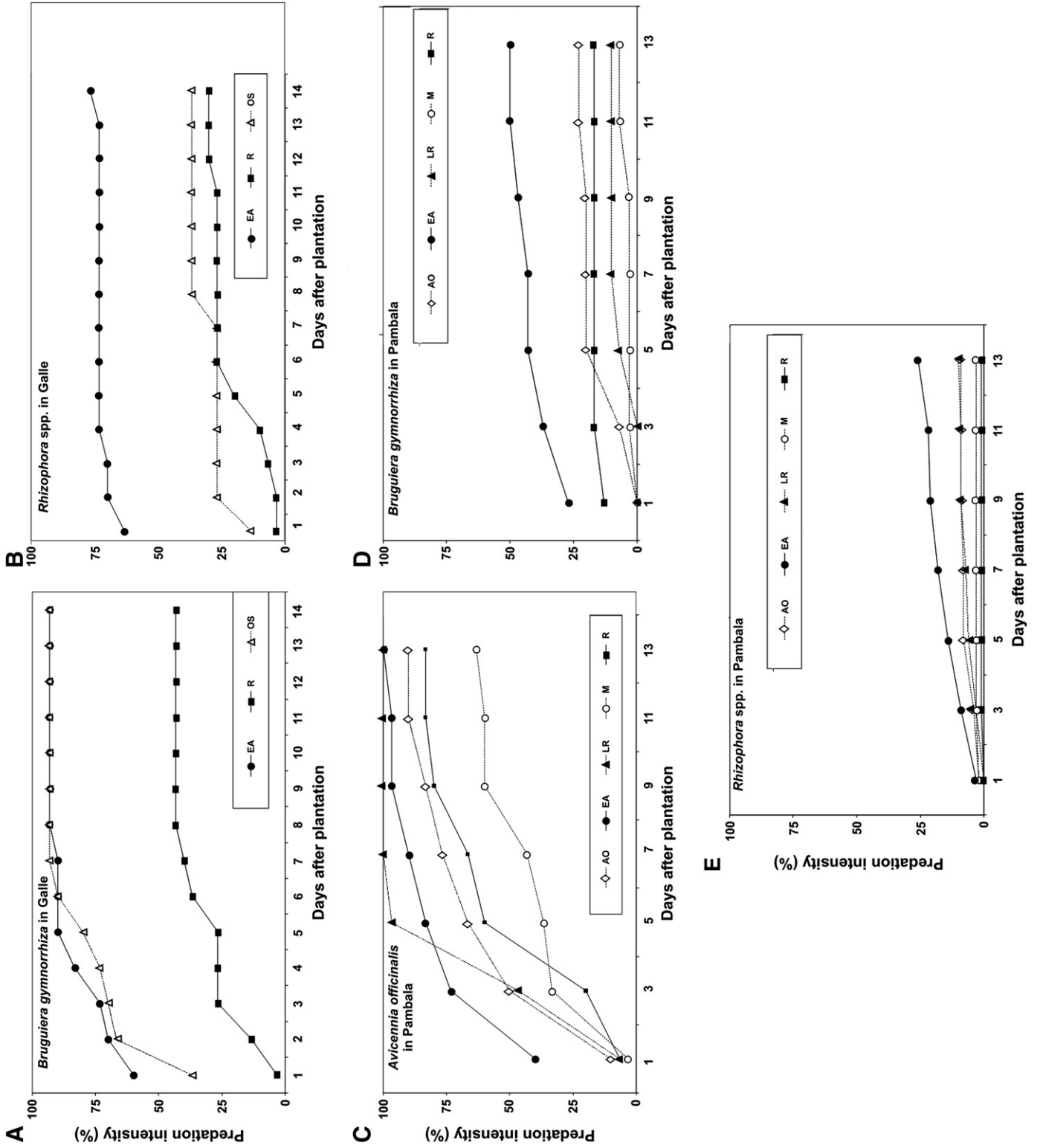
Table 2

Propagule removal. Results from the ANOVA analyses on the percentage of propagules predated within 14 days within and between the different propagule species and forest patches in (a) Galle and in (b) Pambala, (c) between the *E. agallocha* and the *Rhizophora* spp. forest patch of Galle and Pambala, and (d) between the wet and the dry season in Galle.

(a) Source	SS	d.f.	MS	F	p
Propagule species	2570.81	1	2570.81	6.23	0.028
Forest patch	4236.19	2	2118.10	5.14	0.025
Species × forest patch	1433.35	2	716.67	1.74	0.217
Residual	4949.31	12	412.44		
Total	13189.66	17			

SNK post-hoc test on forest patch	Mean ± SE	Mean ± SE	p
E. agallocha vs. open space	74.45 ± 8.36	36.50 ± 5.11	<0.05

(b) Source	SS	d.f.	MS	F	p
Propagule species	32717.91	2	16358.96	69.34	0.000
Forest patch	4650.05	4	1162.51	4.93	0.004
Species × forest patch	1458.35	8	182.29	0.77	0.629
Residual	7077.31	30	235.91		
Total	45903.61	44			

	Mean ± SE	Mean ± SE	p
SNK post-hoc test on propagule sp.			
A. officinalis vs. *B. gymnorrhiza*	76.77 ± 4.83	25.04 ± 5.61	<0.01
A. officinalis vs. *Rhizophora* spp.	76.77 ± 4.83	15.34 ± 2.81	<0.01
SNK post-hoc test on forest patch			
E. agallocha vs. Mixed	56.67 ± 10.6	26.28 ± 9.47	
E. agallocha vs. *Rhizophora* spp.	56.67 ± 10.6	32.71 ± 10.6	

(c) Source	SS	d.f.	MS	F	p
Site	4848.86	1	4848.86	1.54	0.341
Forest patch (site)	6308.91	2	3154.45	9.89	0.002
Propagule species	1487.30	1	1487.30	123.15	0.008
Site × propagule species	113.880	1	113.88	9.43	0.092
Propagule species × forest patch (site)	24.16	2	12.08	0.04	0.963
Residual	5102.45	16	318.90		
Total	17885.54	23			

(d) Source	SS	d.f.	MS	F	p
Season	1392.06	1	1392.06	2.26	0.158
Forest patch	1434.69	2	717.34	1.17	0.344
Season × forest patch	1992.60	2	996.30	1.62	0.238
Residual	7380.34	12	615.03		
Total	12199.69	17			

Table 3

Land/water ratio (dry season), crab burrow density, and density of the snail *T. palustris* in different forest patches of Galle and Pambala. These data were in part taken from Dahdouh-Guebas et al. (2002a).

	Land/water ratio (% land 100 m^{-2})	Crab burrow density (burrows m^{-2})	*T. palustris* density (snails m^{-2})
Forest patches in Galle			
E. agallocha	43.3	3.5	1.9
Open space	9.8	1.3	2.8[a]
Rhizophora spp.	27.4	4.5	0.8
Forest patches in Pambala			
A. officinalis	95.0	5.0	0.0
E. agallocha	95.0	>10.0	0.0
L. racemosa	91.1	6.8	0.0
Mixed	85.0	3.2	0.0
Rhizophora spp.	89.0	2.0	0.0

[a] On bare mud the density of snails can reach ten times this value.

3.3. Biotic and abiotic environmental factors

The land/water ratio reflects the more irregular topography in Galle with many water pools and mud mounts, whereas in Pambala a rather non-sloping plateau is present (Table 3). In Pambala, the general pattern is a lower predation at higher water levels. Since the sesarmid propagule predators are the same in Galle, there is no reason to expect a different pattern in Galle. However, as will be demonstrated later, the incidence of higher water levels was artificially low and therefore the predation pattern cannot always be tested. The relationship between predation intensity and lagoon water level was strong for all species in all forest patches, with r^2 ranging from 0.716 to 0.957 (Table 4).

We highlight here that, first, between day 1, 2 or 3 and day 5, 6 or 7 after the initiation of the experiments in Pambala, a considerable drop in water level of more than 30 cm occurred, before which many crabs were observed to retreat vertically on the mangrove roots, above the water level. Second, parallel with the drop in water level, an increase in propagule predation was recorded for all species in all five forest patches, which is most clear for predation on *A. officinalis*. It is important to recall at this point, first, that the date of the initiation of the experiments is not the same for each forest patch due to the size of the forest — visual combination of the data on water level, which is similar in all forest patches at a particular time, and on predation intensity is therefore not advisable. Second, the earlier mentioned discrepancy was corrected for in the regressions by using experimental days rather than dates, and by excluding the day of plantation itself. Considering that the water level is a date-dependent variable and the experiments were initiated on different days because of the size of the forest, and considering that the predation intensity is a cumulative figure, the original replicas for each of the forest patches were considered again and checked whether a peak in rate of predation corresponded with a lower water level, and thus a greater accessibility of predators to the propagules. For all the *A. officinalis* propagules, and for *B. gymnorrhiza* and *Rhizophora* spp. propagules in the *A. officinalis* and the *E. agallocha* forest patches, these events always coincided.

The data on vegetation structure, and the numerical data of propagule predation after two weeks allowed an easy test of the dominance-predation hypothesis (Table 5). Keeping in mind that other species present were not included mainly because of the low availability of propagules and seeds, it appeared that the dominance-predation hypothesis was only valid with respect to the *A. officinalis* adult trees in the mixed forest patch and for the *A. officinalis* and *Rhizophora* spp. adult trees in the *Rhizophora* spp. forest patch in Pambala: for adult *A. officinalis* its high predation coincided with a low importance value in the tree layer, whereas for *Rhizophora* spp. its low predation coincided with a high importance value (Table 5b). The

analyses were based on the predation intensities after 14 days (Table 2). In both sites there was a significantly different predation between species and between forest patches (Table 2a,b). We detected in Galle a significantly higher predation intensity on *B. gymnorrhiza* regardless of the forest patch in which they were, and a stronger predation in the *E. agallocha* forest patch with respect to the open space patches (Table 2a). In Pambala, the SNK test revealed that the predation was significantly higher in the *E. agallocha* forest patch than in the 'mixed' forest patch and in the *Rhizophora* forest patch, whereas all other differences resulted not significant (Table 2b). With respect to the species it came out that *A. officinalis* was predated more than *B. gymnorrhiza* and than *Rhizophora* spp., but no differences were found between the latter two species (Table 2b). There was no significant interaction between the factor 'forest patch' and the factor 'species', *i.e.* the general trend of predation among the different species is the same throughout the forest patches (Table 2b; Fig. 2). When confronting the forest patches dominated by the same genera among sites, we observed a significantly higher predation on *B. gymnorrhiza* than on *Rhizophora* sp. in both sites (Table 2c). There were no differences between the predation intensities of the dry and the wet seasons (Table 2d).

Table 4
Statistics for the linear relationship between predation intensity (%) and lagoon water level (cm) in Pambala. The various combinations of forest patches for a particular species in the first column reflect the significant differences in predation intensity between forest patches outlined in the text and in Table 2. An asterisk indicates a significant relationship.

Predation intensity	r^2	Equation	n	p-value
A. off in AO, LR, M and R	0.913	$y = -2.0814 \times + 123.79$	5	0.00*
A. off in EA	0.716	$y = -1.0511 \times + 114.93$	5	0.05*
B. gym in AO, LR, M and R	0.920	$y = -0.2701 \times + 16.177$	5	0.00*
B. gym in EA	0.763	$y = -0.37 \times + 30.467$	5	0.04*
R. spp. in AO, LR, M and R	0.887	$y = -0.1731 \times + 11.507$	5	0.00*
R. spp. in EA	0.922	$y = -0.5706 \times + 40.435$	5	0.00*

Propagules: A. off = A. officinalis; B. gym = B. gymnorrhiza; and R. spp. = Rhizophora spp. Forest patches: AO = A. officinalis; EA = E. agallocha; LR = L. racemosa; M = mixed; and R = Rhizophora spp.

'dominance-predation hypothesis' was introduced as an explanation of canopy species dominance, and thus adult abundance. However, we also tested the similar model for the understory trees. The biotic and abiotic factors that can prevent these understory trees to become dominant in the canopy did not compromise the testing of the dominance-predation hypothesis, since the understory trees had survived already beyond the predation threat. Only the *Rhizophora* spp. forest patch in Galle (Table 5a) and the *Rhizophora* spp. forest patch in Pambala (Table 5b) could be identified as forest patches where the 'dominance-predation hypothesis' is valid for some species in the younger understory. Cases in which species displayed a high predation intensity in an area where the species was dominant, or a low predation intensity in an area where the species was not dominant, evidently do not follow the 'dominance-predation hypothesis'.

3.4. Simulating historical lagoon water level (and predation settings)

For Galle, a significant relationship of the water level as a function of rainfall arises when these two types of environmental data are combined monthly ($y = 12.025 \times - 1302.1$; $n = 29$; $r^2 = 0.425$; $p < 0.01$) (Fig. 3). Based on the results from measurements with respect to the water level we concluded that in the present conditions an average monthly water level of 140 cm or above is likely to flood the mangrove forest in such a way that the different sections of the forest are connected and more propagules can float away easily (note from Table 3 that within the forest at Galle the percentage of water is high: between 53 and 91%, which is a lot for a mangrove area at low tide). This threshold figure of 140 cm was based on the difference between the height of the dam (200 cm), and the height of the raised path with respect to the mangrove floor (>60 cm). This means that the water level has to reach the 140 cm threshold to go over the inclinated path and then flood the mangrove in such a way that the different sectors of the mangrove are connected through water. On the other hand, an average monthly water level of less than 120 cm (measured at the dam) was likely to leave a considerable part of the mangrove forest emerged (but some pools and small islands are always present), rather preventing propagules from floating away easily and increasing the probability of predation. Apart from our measurements (Table 3), it is virtually impossible to estimate the surface of the emerged area, unless digital terrain models are available. In addition, the emerged area depends on water level and topography, the latter of which is heavily influenced by the mangrove mud lobster (Di Nitto, 2010). It must be noted also that single flooding events were not necessarily reflected in the monthly average, and could occur as an exception to the above trend (Fig. 3), with extraordinary movement of stranded propagules as a consequence.

Retrospective investigation of the trend in the monthly water level, based on the earlier mentioned relationship with the rainfall data, shows that there were only 2 flooding months (1.1% of the months) since the raised path through the mangroves and the dam were built in 1985 (Fig. 4C). In other words, during this period, only two months displayed an amount of rainfall that was high enough to have the water level exceed the threshold of 140 cm. Before that time (1949–1984), only 5 flooding months were recorded (1.2% of the months) with the above threshold of 140 cm. However, under absence of anthropogenic features that have a strong impact on the hydrology, such as the path or dam, the limit of 140 cm would evidently be too high. Therefore we calculated for each 2 cm increase in barrier height between 100 cm (the minimum water level ever recorded) and 140 cm (the current height of the path) whether or not the lagoon water level would have led to a flooding of the forest. Fig. 4A shows that at 100 cm, which is enough to flood the forest under a lesser degree of human disturbance based on present observations (100 cm is the absolute minimum water level recorded over the period 1997–1999), the proportion of flooding months was obviously 100% (Fig. 4B). We estimate that even before the building of the path and dam flooding indeed occurred at 100 cm. At an intermediate level of 120 cm Fig. 4A shows that flooding occurred in no less than 95.0% of the months (Fig. 4C). Note that 120 cm as an intermediate level is still a very conservative figure to reflect an estimated past condition with no raised path or dam or no other human or natural structures expected to lift the mangrove soil 20 cm and create a barrier that effectively circled the mangroves and thus prevented it from being flooded.

4. Discussion

4.1. Herbivores and predators

The results from this study show that propagule predation in Sri Lanka is not an occasional phenomenon and that grapsid crabs and snails are the main predators once the propagules fall. Various phytophagous insects were reported for mangroves in Thailand (Murphy, 1990; Murphy and Meepol, 1990; Murphy and Rau, 1990; Rau and Murphy, 1990), and Colombia (Elster et al., 1999), but they were clearly not exhaustive for the local forest. Farnsworth and Ellison (1997) claimed that grapsid crabs, coleoptera and lepidoptera were the primary pre-dispersal predators of propagules in the mangroves globally. Ellison and Farnsworth (1993) reported that predation on *Rhizophora mangle* L. by a lepidopteran did not significantly affect plant growth. Predation on *B. gymnorrhiza* by adults and larvae of beetles (Curculionidae, Scolytidae) and by dipteran larvae have been reported before by Robertson et al. (1990), but contrary to our observations their experimental results indicated no adverse propagule growth or survival effects from these insects. Similarly, the colonization of boring insects on propagules with no damage to the seedling's survival was reported by Krauss and Allen (2003). Also, scolytid beetles were found to infest mangrove propagules of the Rhizophoraceae family, in particular *Rhizophora* spp., to such a degree that they could affect the community structure (B. Brook, pers. comm. 2000; Onuf et al., 1977; Sousa et al., 2003). Most recently, land crabs are referred to as the key drivers in tree establishment and recruitment of the tropical coastal forests (*i.e.* mangroves, island maritime forests and mainland coastal terrestrial forests) (Lindquist et al., 2009).

The predation of propagules by *T. palustris* has been reported by Plaziat (1984), Fratini et al. (2004), and Bosire et al. (2008) among others. Contrary to observations on the same gastropod in Kenya during earlier studies (Dahdouh-Guebas et al., 1998), where the specimens cut through the hypocotyl first, propagules consumed by this gastropod in Sri Lanka had the epicotyl scraped off first in most cases. In a few cases the hypocotyl was affected only later or not at all.

Table 5

Relative density (De$_r$), relative frequency (F$_r$), relative dominance (Do$_r$) and the importance value (I.V.) of Curtis (1959) from Point Centred Quarter Method (PCQM) transects on adult trees, young trees, and juveniles (propagule producing species) from 1997, 1998 and 1999 for the main forest patches in (a) Galle (Dahdouh-Guebas et al., 2000) and (b) Pambala (Zetterström, 1998; Dahdouh-Guebas, unpublished results). Also the predation intensity for each experimental species is given per forest patch (in the bottom lines of the table), and shaded areas indicate a positive relationship with the 'dominance-predation hypothesis', *i.e.* high predation intensity coinciding with a low I.V., or *vice versa*. Species abbreviations follow those in Table 4.

(a) Galle	E. agallocha				Open space				Rhizophora spp.			
	De$_r$	F$_r$	Do$_r$	I.V.	De$_r$	F$_r$	Do$_r$	I.V.	De$_r$	F$_r$	Do$_r$	I.V.
Adult trees												
Bruguiera gymnorrhiza	8.2	14.3	3.7	26	5.1	9.8	4.2	19	2.9	2.6	5.6	11
Rhizophora spp.	16.9	22.9	17.0	57	8.9	9.8	8.1	27	51.4	52.3	44.4	148
Other species	74.9	62.9	79.3	217	86.1	80.5	87.7	254	45.7	45.1	50.0	141
Young trees												
Bruguiera gymnorrhiza	70.6	62.5		133	14.6	24		39	46.7	39.5		85
Rhizophora spp.	4.8	8.3		13	8.3	12		20	33.3	38.5		72
Other species	24.6	29.2		54	77.1	64		141	20	23		43
Propagules 01/1997												
Bruguiera gymnorrhiza	13.6	22.2		36	1	16.7		18	0.7	16.7		17
Rhizophora spp.	86	66.7		153	47.3	50		97	78.9	50		129
Other species	0.3	11.1		11	51.7	33.3		85	20.4	33.3		54
Propagules 03/1998												
Bruguiera gymnorrhiza	98.5	61.8		160	87.4	62.5		150	83.1	41.7		125
Rhizophora spp.	1.1	29.4		31	12.6	37.5		50	16.9	58.3		75
Other species	0.4	7.8		8	0	0		0	0	0		0
Propagules 11/1999												
Bruguiera gymnorrhiza	20.7	40.4		61	30.4	53.8		84	0.1	9.5		10
Rhizophora spp.	79.3	54.4		134	69.6	46.2		116	99.9	90.5		190
Other species	0	5.3		5.3	0	0		0	0	0		0
Predation intensity after 14 days for…												
…*Bruguiera gymnorrhiza*		93%				93%				43%		
…*Rhizophora spp.*		95%				40%				40%		

(b) Pambala	L. racemosa				Mixed				Rhizophora spp.			
	De$_r$	F$_r$	Do$_r$	I.V.	De$_r$	F$_r$	Do$_r$	I.V.	De$_r$	F$_r$	Do$_r$	I.V.
Adult trees												
A. officinalis	7.0	11.1	4.4	22	2.3	3.4	2.8	9	3.8	5.5	4.0	13
B. gymnorrhiza	1.6	3.7	1.2	6	14.0	20.7	50.8	37	3.0	5.5	0.9	9
Rhizophora spp.	0.8	3.7	0.6	5	4.7	3.4	4.0	12	75.5	64.2	91.8	232
Other species	90.7	81.5	93.8	266	79.1	72.4	90.3	242	17.7	24.8	3.3	46
Young trees												
A. officinalis	14.9	15.6		31	0.0	0.0		0	8.5	10.7		19
B. gymnorrhiza	6.4	6.3		13	25.6	23.8		50	3.7	5.4		9
Rhizophora spp.	0.0	0.0		0	0.0	0.0		0	39.0	37.5		77
Other species	78.7	78.1		157	74.2	76.2		150	48.8	46.4		95
Propagules 02/1997												
A. officinalis	82.2	66.7		155	93.8	75.0		169	8.2	10.1		18
B. gymnorrhiza	0.0	0.0		0	0.0	0.0		0	0.1	3.8		4
Rhizophora spp.	0.0	0.0		0	0.0	0.0		0	79.9	45.6		126
Other species	11.8	33.3		45	6.3	25.0		31	11.9	40.5		52
Propagules 04/1998												
A. officinalis	83.3	50		133	0.0	0.0		0	58.2	16.9		75
B. gymnorrhiza	0.0	0.0		0	58.2	66.7		155	0.0	3.4		3
Rhizophora spp.	16.7	50.0		67	0.0	0.0		0	41.1	55.9		97
Other species	0.0	0.0		0	11.8	33.3		45	0.6	23.7		24
Propagules 11/1999												
A. officinalis	94.2	55.6		150	5.2	28.6		34	15.5	17.2		33
B. gymnorrhiza	0.0	0.0		0	1.3	14.3		16	0.0	6.1		6
Rhizophora spp.	3.4	11.1		14	0.0	0.0		0	83.5	46.5		130
Other species	2.4	33.3		36	9.5	57.1		151	1.0	30.3		31
Predation intensity after 13 days for…												
…*A. officinalis*		100%				63%				83%		
…*B. gymnorrhiza*		10%				7%				17%		
…*Rhizophora spp.*		13%				5%				2%		

4.2. Differential predation patterns

Many of the observed differences among species and forest patches can be explained by the abundance of propagule predators. The significantly higher predation in the *E. agallocha* forest patch is probably in part due to the relatively high density of crabs (Table 3). However, although burrow counts often overestimate the actual crab population (Crane, 1975; Frith and Brunenmeister, 1980; Skov et al., 2002; Bosire et al., 2004), the density of crabs alone cannot account for the significantly higher predation intensity. Rather than crab density (which is an average for the entire forest patch), local individual crab intensity of predation on propagules resulting from the micro-topography is suggested to play a role in this observation. In Galle, the highly irregular topography, which forms a mosaic of pools and small islands built by *T. anomala*, concentrates predators on the emerged locations and must also increase the intensity of predation. This situation leads to a fast predation on whichever propagule
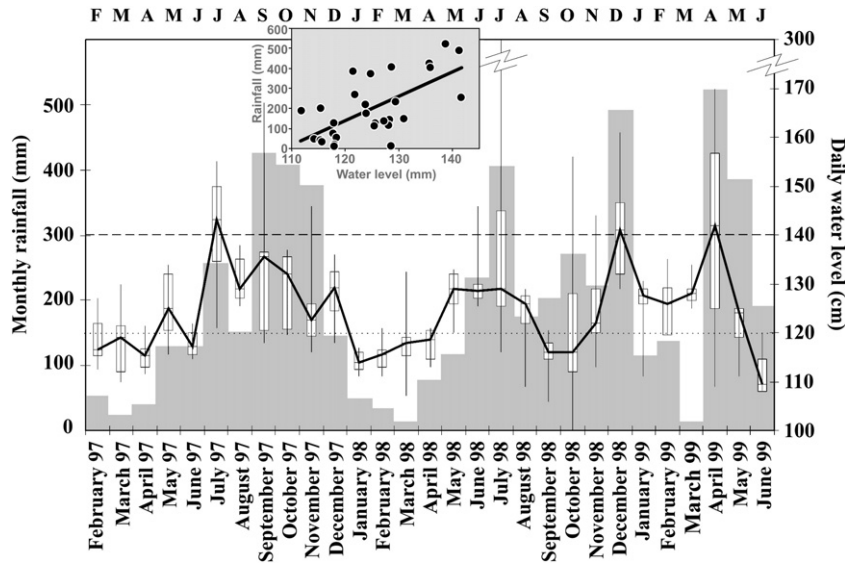
Fig. 3. Monthly rainfall (grey histograms) and water level (solid line) measured at the concrete dam in the Galu Ganga in the mangrove forest of Galle between 24/01/1997 and 21/07/1999. The water level fluctuations within each month are summarized by a box plot indicating minimum (lower line), maximum (upper line), 50% of the data (rectangular box), and the median (small horizontal line within the box). The dashed horizontal line throughout the graph indicates the minimum average monthly water level at which propagules are likely to float away, whereas the dotted horizontal line indicates the maximum average monthly water level at which propagules are likely to be predated (see text for details). The inset shows the correlation and the regression line between the monthly rainfall and the water level ($y = 12.025 \times - 1302.1$; $n = 29$; $r^2 = 0.425$; $p < 0.01$).

is accessible, and to a behaviour concerning propagule predation of multiple plant species that has also been observed in high density areas in Kenya for *N. meinerti* (Dahdouh-Guebas et al., 1997) and other sesarmids (Dahdouh-Guebas et al., 1998).

For Pambala, the relatively higher predation on *A. officinalis* is in agreement with the results on the same genus elsewhere (McKee, 1995; McGuinness, 1997b; Sousa and Mitchell, 1999; Minchinton and

Dalby-Ball, 2001; Clarke and Kerrigan, 2002), but the dominance-predation hypothesis, which was supported by the results on *Avicennia* in Australia, Malaysia, Florida and Panama (Smith et al., 1989), is rejected (Table 5b), as it was by McKee (1995), McGuinness (1997b) and Sousa and Mitchell (1999). The high predation must be the result of either a preference (*i.e.* selection of specific propagule) (cf. Skov and Hartnoll, 2002), whatever the competition situation is,
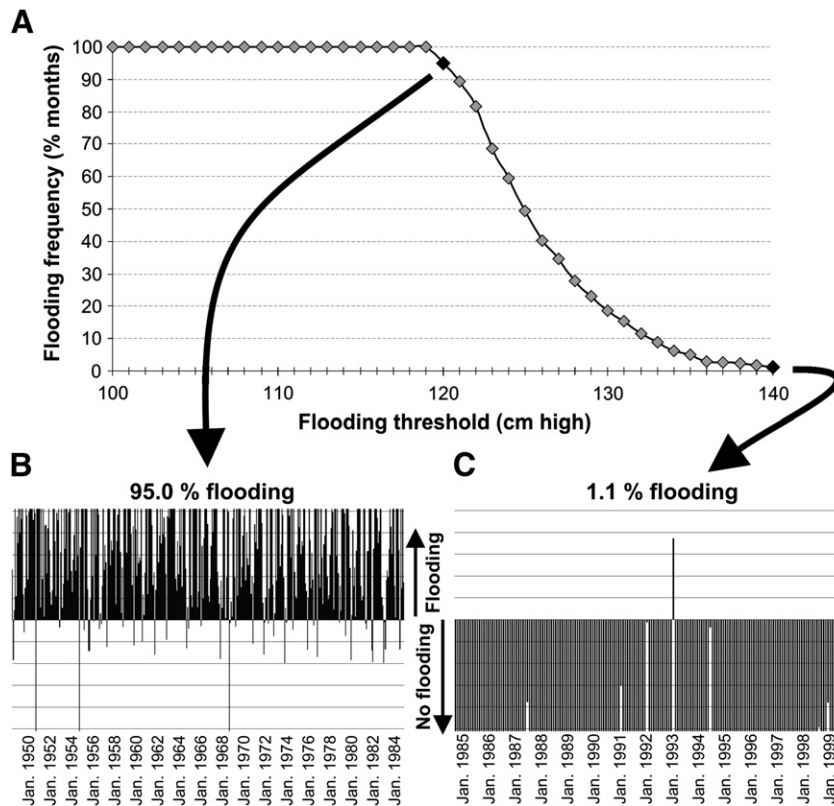
Fig. 4. Frequency of flooding (in months) of the mangrove in Galle with respect to a changing flooding threshold (A). The proportion of flooding months and non-flooding months are indicated in a histogram with the X-axis intersecting at (B) a threshold of 120 cm (before dam construction), and (C) a threshold of 140 cm (present condition with raised path and dam). Each horizontal gridline in histograms B and C corresponds to a height difference of 1 cm; water levels >5 cm above or <5 cm below the threshold are off the chart. See text for full details.

or an ease of propagule handling by the predator because of the small size and compact shape. For Galle, the significantly higher predation on *B. gymnorrhiza*, with the smaller propagules, may also indicate that propagule size or post-fall position (vertical or horizontal, horizontal propagules being easier to evacuate) matters. The significantly higher predation in the *E. agallocha* can also be linked directly to crab abundance. Considering the rather high abundance of crabs in the *L. racemosa* forest patch, the absence of a significantly higher predation on all species may be explained by the fact that this forest patch seldom receives a natural input of propagules from *Bruguiera* or *Rhizophora* species. A second explanation is that as a result of the absence of *T. anomala* in Pambala, the forest patches are more contiguous and the propagule predators are more spread, with exception of the *Excoecaria* forest patch, which is still elevated naturally and often surrounded by water (like in Galle). A biotic factor that plays a role in propagule predation in general is the presence of *T. palustris*. This species is known to consume mangrove propagules (Slim et al., 1997; Dahdouh-Guebas et al., 1998). Finally, in Pambala the most predated species (100% predated after 13 days) was *A. officinalis*, a species not present in Galle. The lower predation rates on the other species in Pambala, as observed, can be due to the possibility that the predators invest their energy fully in predating *Avicennia*.

In a few cases only (3 out of 15 and 4 out of 15 for adult and young tree layers respectively) the pattern of differences in propagule predation among forest patches indicated that propagule predators could determine the distribution of the mangroves species according to the dominance-predation hypothesis (Smith, 1987a, 1987b). So this hypothesis remains a possible link in the chain of factors that shape vegetation structure in certain areas. Where valid for understory vegetation, the dominance-predation hypothesis in the present study does not necessarily remain valid for the adult vegetation layer (*e.g. Rhizophora* spp. forest patch in Galle). Only long-term monitoring of the established propagules will show which biotic or abiotic factors will further determine their survival.

4.3. Influence of environmental factors on predation

From all environmental variables measured, water level of the lagoon in Pambala has the best relationship with the predation data. This leads to the hypothesis that propagule predation and vegetation structure dynamics in areas without a topographic gradient and that are influenced little by tidal effects, can be largely controlled by differences in water level in the wet and dry seasons. Keeping in mind the relation between rainfall, water level and predation (see Results) we note that in the *E. agallocha* forest patch, predation on *A. officinalis* occurred right from the start of the experiment, thus before the drop in water level. This can be explained by this forest patch occupying the highest topographic levels, which are seldom, if ever, submerged. Nevertheless, there is also a significant relation between predation intensity and water level, except for *A. officinalis*. The latter can be explained by the small size of the propagule (*Avicennia* has small oval-shaped propagules of about 2–3 cm large, as opposed to representatives of the Rhizophoraceae having long torpedo-shaped propagules that may be as large as 20 cm in *Bruguiera* and 50 cm in *Rhizophora*), or by the higher preference the crabs have for this propagule.

Dahdouh-Guebas (2002) defined 'biocomplexity' as 'the complexity of the interactions between biodiversity (fauna and flora), the environment and man, and of ecosystem functioning, and the complexity of their regulation, within an ecosystem but also among interlinked ecosystems (particularly in tropical coastal environments). Cannicci et al. (2008) illustrated how a 'spatio-temporal biocomplexity model' may be at the origin of the observed differential patterns in vegetation structure through a chain of events including propagule predation. We must, however, depart from a number of rather evident conjectures that are may be valid for the entire forest area: the irregular micro-topography remains constant, the presence

of propagule predators remains constant, their feeding behaviour remains constant, the provision of food for them remains constant, and there are no unknown underwater propagule predators. It is obvious that if one or more of these conjectures change, this will result in an altered propagule predation.

4.4. Effects of historical hydrographical changes on propagule predation

Although at the time of the predation experiments the water level was permanently low in Galle, occasional flooding of the entire mangrove forest (including the dam and the raised path) was observed during the rainy season. The daily and seasonal water level fluctuations observed in the present study are in line with the spatio-temporal biocomplexity model explaining the role of propagule predators in the shaping of vegetation structure under different inundation regimes (Cannicci et al., 2008). In fact, what we permanently observe in Galle is a higher predation intensity (possibly due to competition) on the islands, which is in line with their theory. The extrapolation (based on real data) to past conditions indicates that the impact of anthropological constructions on the hydrography of the system was great enough to alter the frequency of flooding events by decreasing the number of months with flooding as a result of dam and path constructions. Since flooding plays a regulatory role in the interaction between propagule predation and dispersion (Jiménez and Sauter, 1991; Di Nitto et al., 2008), it follows that propagule predation may be regulated by man indirectly in our study area. Indirect anthropogenic effects thus may affect apparently natural biological processes such as propagule predation, which is not an *a priori* evidence.

Our results suggest that spatial and temporal microhabitat variations give way to multiple successional pathways in vegetation structure dynamics. On one hand, spatial microhabitat variation in the present study is determined by the presence of animal species that drastically alter the microtopography within the forest (*T. anomala*) and induce variability in environmental conditions, to which floristic assemblages respond (therefore interacting with their succession). Temporal microhabitat variation, on the other hand, is here determined by human influences that affect local and seasonal hydrology and other environmental factors. Hydrochory, which is common in mangrove species, and stranding of propagules, will evidently be influenced by a changed hydrography, hydrology and microtopography. For instance, the ability for *Rhizophora* root complexes to entangle propagules decreases with a higher water level (see also Dahdouh-Guebas and Koedam, 2006a; Di Nitto et al., 2008). Also the terrestrialisation of elevated areas in the mangrove forest influences the dispersal of propagules, with more predators in dense, closed canopies than in open ones. In fact, under such conditions in monospecific reaforested mangroves areas in Kenya, sesarmid propagule predators have also been found to regulate forest regeneration (Bosire et al., 2005). 'Cryptic ecological degradation' (*sensu* Dahdouh-Guebas et al., 2005a), a phenomenon in which typical, vulnerable, functional, and valuable true mangrove species are gradually being replaced by introgressive mangrove-associated vegetation or minor mangrove species (less typical, less valuable, and less vulnerable) (qualitative degradation), but without loss of spatial extent (no change or an increase in area), may further influence the survival of propagules, the succession of species assemblages and eventually the functionality of the mangrove forest (Dahdouh-Guebas et al., 2005b; Dahdouh-Guebas and Koedam, 2006b). This spatio-temporal complexity shows that the direct origin of certain changes in the environment can be evident (*e.g.* the increase in the abundance of *T. anomala*), but also that the chain of interaction and synergism can be traced to distal factors (such as hydrographical works).

Theories on the establishment of vegetation structure often exclusively focus on the effect of direct and measureable proximate factors (for example Clarke et al., 2001). This study shows that even in

processes that are seemingly natural, less apparent distal factors drive the behaviour of propagule predators. We evidenced a new climatic link in propagule predation and in the role that propagule predators play in the shaping of a vegetation structure. We confirmed that propagule predation remains an important eliminator of propagules also in areas with little tidal influence and a mosaic patchy vegetation structure (as compared to systems with a large tidal amplitude), but that the incidence of propagule predation is regulated by stochastic or seasonal processes such as propagule falling, rainfall, inundation (water level), and human influence (see also Cannicci et al., 2008). The study of the link between propagule dispersion, topography and inundation regimes using digital terrain models and hydrological modelling is very promising in this respect (Di Nitto et al., 2008; Di Nitto, 2010).

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