Review

Faunal impact on vegetation structure and ecosystem function in mangrove forests: A review

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Abstract

The last 20 years witnessed a real paradigm shift concerning the impact of biotic factors on ecosystem functions as well as on vegetation structure of mangrove forests. Before this small scientific revolution took place, structural aspects of mangrove forests were viewed to be the result of abiotic processes acting from the bottom-up, while, at ecosystem level, the outwelling hypothesis stated that mangroves primary production was removed via tidal action and carried to adjacent nearshore ecosystems where it fuelled detrital based food-webs. The sesarmid crabs were the first macrofaunal taxon to be considered a main actor in mangrove structuring processes, thanks to a number of studies carried out in the Indo-Pacific forests in the late 1970s and early 1980s. Following these classical papers, a number of studies on Sesarmidae feeding and burrowing ecology were carried out, which leave no doubts about the great importance of these herbivorous crabs in structuring and functioning Old world ecosystems. Although Sesarmidae are still considered very important in shaping mangrove structure and functioning, recent literature emphasizes the significance of other invertebrates. The Ocypodidae have now been shown to have the same role as Sesarmidae in terms of retention of forest products and organic matter processing in New world mangroves. In both New and Old world mangroves, crabs process large amounts of algal primary production, contribute consistently to retention of mangrove production and as ecosystem engineers, change particle size distribution and enhance soil aeration. Our understanding of the strong impact of gastropods, by means of high intake rates of mangrove products and differential consumption of propagules, has changed only recently. The role of insects must also be stressed. It is now clear that older techniques used to assess herbivory rates by insects strongly underestimate their impact, both in case of leaf eating and wood boring species and that herbivorous insects can potentially play a strong role in many aspects of mangrove ecology. Moreover, researchers only recently realized that ant–plant interactions may form an important contribution to our understanding of insect–plant dynamics in these habitats. Ants seem to be able to relieve mangroves from important herbivores such as many insects and sesarmid crabs. It thus seems likely that ants have positive effects on mangrove performance.
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Contents

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1. Introduction

During the past 20 years a paradigm shift has occurred concerning ideas about factors influencing mangrove forest structure and ecosystem dynamics. Prior to the 1980s, structural aspects of mangrove forests (e.g. species richness, plant distribution patterns, productivity, biomass) were viewed to be the result of abiotic processes acting from the bottom-up. Forces such as frequency and duration of tidal flooding, salinity, and sediment characteristics (nutrient availability, redox) were viewed as the primary drivers (see Smith, 1994 for a review). This view also existed at the ecosystem level. The outwelling hypothesis stated that mangrove primary production was removed via tidal action and carried to adjacent nearshore ecosystems where it fuelled detrital based food-webs (Odum, 1971; Odum and Heald, 1972,1975).

In the late 1970s and early 1980s a number of studies appeared indicating that biotic factors were important to shape mangrove forests vegetation structure and ecological processes occurring in them. Working in Florida, Beever et al. (1979) demonstrated that herbivory by the arboreal grapsid crab, *Aratus pisonii* (H. Milne Edwards), played a role in the energy flow of mangroves and that export of material via crab biomass could be significant. In Australia, Robertson (1986) demonstrated that crabs had significant impacts on energy flow and export from mangroves, while Smith (1987) showed that, by consuming mangrove propagules, crabs could influence forest structure. Subsequent experimental work revealed that burrowing by crabs had significant effects on sediment chemistry and forest productivity (Smith et al., 1991).

The foundation for the idea of crabs as ecosystem engineers had just been laid when other invertebrate taxa, such as molluscs and insects, went on the stage. In fact, Bouillon et al. (2002a,b), using carbon and nitrogen stable isotope signatures, showed that molluscs' overall consumption of mangrove litter in some Indo-Pacific mangrove forests, and consequent contribution in nutrient dynamics, can be much higher than that of sesarmid crabs. Molluscs can reach an astonishingly high biomass in mangroves and they occupy very different levels of the ecosystem food web. While gastropods contribute to entrap primary production within the system, both grazing fallen leaves and consuming mud (mainly composed by mangrove litter), bivalves are efficient filter feeders, able to capture suspended particles of various origins (Plaziat, 1984; Kathiresan and Bingham, 2001).

In virtually all forest ecosystems, insects have a significant impact on tree growth rate and form, survivorship, reproductive output and forest ecology (Schowalter, 1986; Crawley, 1989), however, the impact by insects on mangroves has been considered of minor importance compared to other types of forests (Macnae, 1968). However, an increasing focus on mangrove herbivory has shown that the situation is not different in mangroves. Being dominated by trees, mangroves forests are similar to terrestrial forests in many ways, this being especially so for canopy fauna such as insects. In a thorough review, Burrows (2003) found no evidence that mangrove trees in general had lower levels of herbivory than tree species elsewhere, with any differences being attributable to individual species characteristics rather than a general feature of mangrove forests.

Among the insects, ants play an important ecological role. Their high abundance and the multitude of interactions they are engaged in make them important actors in ecosystem functioning (Wilson, 1959; Beattie, 1985; Hölldobler and Wilson, 1990). From terrestrial studies it is well documented that ants are able to protect plants against herbivores via their predatory and territorial behaviour (reviewed by Bronstein, 1998). Only few studies have dealt with mangrove ants. These

suggest that densities may be lower than in terrestrial habitats, but still ants are among the most numerous groups of animals (Simberloff and Wilson, 1969; Clay and Andersen, 1996; Cogni et al., 2003; Dejean et al., 2003). The general picture that emerges from the present mangrove ant studies is that ants have a significant effect on the plant community via their interactions with herbivores. Moreover, some new and fascinating ant–plant protection interactions have been revealed in the mangrove (Offenberg, 2004). For example, Offenberg et al. (2006a) showed that ants indirectly, via their protection against leaf beetle folivory, protect mangrove trees against male crab grazing but not against grazing by female crabs.

The few examples sketched above show how macrofaunal assemblages were only recently considered of major importance in shaping mangrove ecosystem structure and function. The present paper is thus aiming to review the ecological role of the main actors among the faunal taxa, trying to depict what is now known and what we still need to clarify on the importance of biotic impacts on mangrove ecosystems.

2. Insects

2.1. Herbivorous insects in mangroves

2.1.1. Leaf-feeders

The most common forms of insect herbivory are leaf-feeding, wood-boring and flower/fruit/seed-feeding. Leaf-feeding has been most studied in mangroves and the dominant means of assessing this is to measure the amount of leaf area missing or being damaged from a sample of leaves collected from a tree. This discrete technique has been utilised in 20 separate studies in mangroves (reviewed in Burrows, 2003). However, because this method does not account for leaves that are entirely eaten or prematurely abscised because of high damage levels, it significantly underestimates the true level of leaf material lost to herbivores (Lowman, 1984; Landsberg, 1989; Landsberg and Ohmart, 1989; Aide, 1993; Hurley, 1995; Jackson, 1995; Burrows, 2003). Alternative methods of assessing leaf loss have shown that up to 13% of *Rhizophora stylosa* Griff. and 36% of *Avicennia marina* (Forsk.) Vierh. leaf material, can be lost to herbivores (Burrows, 2003), this being 2–5 times greater than estimates usually produced from discrete studies. Although the application of these alternative methods are more time-consuming, they do provide a very different picture of herbivore damage. Instances of mass defoliation events in mangroves (reviewed in Burrows, 2003) are treated as curiosities and are usually only reported anecdotally or in short note form. Three exceptions are from Ecuador (Gara et al., 1990), Hong Kong (Anderson and Lee, 1995) and Queensland, Australia (Duke, 2002), with the latter two including detailed studies of defoliation 'events' that lasted several years. Duke (2002) proposed that such events be considered as a potentially important ecological process and studied in more detail.

The mechanisms by which insects damage mangrove leaves also varies. In the study of Burrows (2003), leaf surface area missing or damaged only comprised one-third of leaf area damaged by insects, with leaf mines, galls and necrosis due to

sap-feeders also major sources of leaf damage. Damage to apical buds and developing leaves can be substantial and in an Australian study of *R. stylosa*, loss of leaf material during the short development phase prior to unfurling from the stipules, was greater than what occurred for the entire lifetime for those leaves that did survive to full emergence (Burrows, 2003). Loss of these apical buds can also reduce reproductive output and leaf production rates, and alter the branching pattern of *Rhizophora* species (Onuf et al., 1977; Murphy, 1990; Anderson and Lee, 1995; Feller, 1995; Burrows, 2003). Insect feeding also causes the premature abscission of heavily damaged leaves. For both *A. marina* and *R. stylosa*, Burrows (2003) found that the amount of leaf area prematurely abscised because of insect damage was equal to or greater than that actually consumed by the insects themselves. Thus an assessment of actual herbivore damage to leaves requires an assessment of leaf area loss over time, other forms of leaf damage, loss of abscised intact leaf material and reduced leaf production.

2.1.2. Wood-borers

Studies of the ecological effect of insect wood-borers in mangroves are limited to those of Feller and Mathis (1997), Feller and McKee (1999) and Feller (2002). For Belizean *Rhizophora mangle* L. forests, these studies have shown that the amount of leaf area lost due to the feeding activities of wood-boring insects (which cause mortality of leaves distal to the point at which the branches are fed upon) was equal to or greater than that lost directly to leaf-feeding insects themselves. Conversely, at one site, Burrows (2003) found that through their destruction of the apical meristem of *R. stylosa* (and subsequent failure of the shoot to produce any new leaves), leaf-feeding herbivores caused greater mortality of woody shoots than wood-borers did. Thus, the mechanisms of herbivore damage are not always obvious and wood-boring may be an unexpected cause.

2.1.3. Effect of herbivory on reproductive output

Analogous to the situation for leaf production, the number of propagules a plant produces may be affected more by reallocation of resources to compensate for herbivore damage elsewhere on the plant, than by actual damage to propagules themselves. Although the degree of herbivore attack in both instances was unusually high, Anderson and Lee (1995) and Tong et al. (2003), showed that defoliation of *A. marina*, and artificial damage to *Kandelia candel* (L.) Druce, significantly reduced propagule production, thus making it a more important form of reduced reproductive output than predation upon the propagules that were actually produced.

Quantification of reduced growth rates and mangrove tree mortality due to herbivores is limited, even for events of mass defoliation. Ozaki et al. (1999) showed that scale insect infestation could cause mortality of *Rhizophora mucronata* Lam. saplings. Most commonly however, studies of mortality and reduced growth rate have been performed on propagules and seedlings. In a rapid global survey of mangrove pre-dispersal propagule predation, Farnsworth and Ellison (1997)

found that insects were the most damaging herbivores. Onuf et al. (1977), Rabinowitz (1977), Robertson et al. (1990), Clarke (1992), Elster et al. (1999), Brook (2001), Minchinton and Dalby-Ball (2001) and Sousa et al. (2003) have all shown high frequencies and levels of insect predation (mainly beetles and caterpillars) upon mangrove propagules, though the subsequent impacts of this attack upon seedling growth and survival are variable.

Elster et al. (1999) found that caterpillars caused substantial mortality (up to 100% at some sites) of *Avicennia germinans* (L.) Stearn propagules and seedlings. Sousa et al. (2003) found that the boring of the scolytid beetle, *Coccotrypes rhizophorae* (Hopkins), into *R. mangle* propagules killed 72–89% of seedlings planted in closed canopy sites (but only 1–2% in adjacent light gaps). These beetles can seriously affect mangrove restoration efforts involving propagules (Kaly and Jones, 1998; Elster et al., 1999). The level of impact on propagules can depend on many factors apart from the amount of damage. These include where the damage occurs (internally boring insects are more damaging, Farnsworth and Ellison, 1997; Minchinton and Dalby-Ball, 2001) and the intertidal and micro-habitat position of the propagule (Robertson et al., 1990).

2.1.4. Costs of herbivore damage

Herbivorous insect impact in itself is often not directly related to the amount of damage caused and certain types and levels of damage may have no effect at all, thus the magnitude of the impact cannot be judged solely from the amount of damage measured. Burrows (2003) and Minchinton and Dalby-Ball (2001) provide mangrove examples of how small amounts of feeding on key parts of leaves and fruit respectively, can have much greater impacts than greater amounts of feeding on less important tissues. In *Rhizophora* for example, small amounts of herbivore damage to the apical buds has much greater effect on leaf survival and retention than larger amounts of damage to leaf lamina (Burrows, 2003).

The costs of anti-herbivore defences need to be weighed against the costs of plant material lost to herbivores. The comparison between *Avicennia* and *Rhizophora* leaves illustrated in Burrows (2003) provides an example. Leaves of *Rhizophora* (and indeed other Rhizophoraceae) are generally larger, thicker and heavier than those of *Avicennia* species, requiring more energy and investment in their construction. For instance, Burrows (2003) found *R. stylosa* leaves to, on average, cover more than twice as much surface area, to be 35% thicker and to have 34% more leaf mass per unit area, than *A. marina* leaves. Thus *Rhizophora* leaves may be more worth defending against herbivore attack than *Avicennia* leaves which would appear to be more expendable. Or put another way, *Avicennia* has a strategy of producing many leaves, each with less investment and thus tolerating high levels of damage, whereas *Rhizophora* produces fewer leaves with greater investment in each leaf. The true cost of herbivore attack is thus the energy lost to herbivore damage plus the energy invested in defending against such loss. Another difference between *Avicennia* and *Rhizophora* is the different ability to recover from damage.

Avicennia has precocious leaf production and if a branch is damaged, many new sprouts soon form, whereas for *Rhizophora*, leaf production is confined to the apical meristem. If that is damaged, suppressed laterals may compensate but as shown by Burrows (2003), this is hardly sufficient, and loss of the apical meristem most commonly results in cessation of leaf production from that shoot, ultimately leading to its death. Thus the two species differ in their ability to recover from insect (and other forms of) damage. Taken together, the most important effect of herbivores on *Rhizophora* may be suppressed leaf production (an effect only detectable through measurement not observation) whereas the more visually obvious consumption of leaf material may be more important in species of *Avicennia*.

The literature in terrestrial forests contains many studies on the costs of anti-herbivore defences and how in times of resource-shortage, these defences may be foregone, rendering plants more susceptible to herbivore attack. This topic has only been addressed in a limited manner for mangroves. An interesting illustration of the point is provided by the observations of McKillup and McKillup (1997). They noted that the blind-your-eye mangrove, *Excoecaria agallocha* L., was rarely attacked by insects but that during a drought, many plants were severely insect attacked, except those who bordered the only remaining sources of fresh groundwater. The paper was only observational, no leaf chemistry was undertaken to support the observations, but it does illustrate the possibility that when stressed, the trees reduced investment in their anti-herbivore defenses, and were subsequently attacked and defoliated. In Sri Lanka, however, leaf herbivory by caterpillars affects 100% of *E. agallocha* leaves every year (pers. obs.). While anti-herbivores defences may decrease when under stress, trees may also respond to insect attack by altering the level of various chemical compounds in leaves that may act to deter insect herbivores. For example, leaf tannins are thought to decrease herbivore feeding activity. Anderson and Lee (1995) showed that although the tannin content of *A marina* leaves attacked by insects during a defoliation event, did not increase, the next cohort of leaves subsequently produced by the trees did have elevated tannin content. Tong et al. (2003) demonstrated that artificially damaged *K. candel* leaves subsequently showed altered leaf chemistry such as decreased nutrient and tannin levels. Although the value of reducing tannin levels is unclear, the decreased leaf nutrient content would be expected to reduce herbivore growth rates and may thus act as a deterrent. Neither study examined insect herbivore damage on leaves after the observed chemical changes, thus leaving the question as to the actual effectiveness of such chemical responses unresolved.

Resource availability can influence herbivore attack not just through anti-herbivore defences but through the attractiveness of plant material. Onuf et al. (1977) reported significantly higher levels of herbivore damage and lost leaf production of *R. mangle* at higher nutrient sites. Feller (1995) showed that herbivory on *R. mangle* trees artificially treated with P and NPK fertiliser significantly increased by some specialists, though not generalists, despite the increase in leaf phenolic compounds that accompanied the fertiliser treatments. Although herbivore damage rate increased, because leaf production rates of the

fertilised trees also increased, the actual proportion of total potential leaf production did not differ between the treatments. This conflicts with the study of Onuf et al. (1977) where an increased rate of leaf production did not keep up with the increased rate of herbivory. However, Onuf et al. (1977) did not provide leaf nutrient content data so the relative degree of fertilisation between the two studies cannot be compared.

2.2. Ants in mangroves

Ants are numerous in terrestrial habitats and are probably the group of insects that has the highest ecological impact in many ecosystems since they can make up more than 10% of the faunal biomass (Wilson, 1959; Hölldobler and Wilson, 1990). They play an important role via their various interactions with plants. Disregarding leaf cutter and harvester ants, most ant–plant interactions are beneficial to plants. They include ants providing nutrients to plants, pollination, seed dispersal and protection against herbivory (Beattie, 1985). In return plants provide easily collectable food and/or hollow structures where the ants can nest (Beattie, 1985). Thus, despite indirect negative impacts from ants, such as the tending of herbivorous homopterans (Way, 1963), many plant species invest in strategies to attract ant partners and the net outcome in most cases is considered to be positive (Bronstein, 1998).

Most ants are ground dwelling and therefore face considerable problems getting established in the regularly flooded mangroves. Even so, they remain the most dominant insects in this habitat (Clay and Andersen, 1996; Dejean et al., 2003) both numerically and energetically (Simberloff and Wilson, 1969). The mangrove ant fauna is composed of terrestrial species as well as species endemic to mangroves. Though a few species have adapted to nest in the flooded sediment (Clay and Andersen, 1996; Nielsen, 1997a,b; Nielsen et al., 2003a,b), compared to terrestrial habitats, the species composition is skewed toward arboreal species (Clay and Andersen, 1996; Nielsen, 2000; Wetterer and O'hara, 2002; Cogni et al., 2003; Dejean et al., 2003). The predominant arboreal life style, though, may favor ant protection since ants are constrained to forage on plants.

2.2.1. Ants impact on mangrove herbivores

Mangrove ant studies have largely dealt with four major topics: (i) species surveys investigating distribution (Simberloff and Wilson, 1969; Cole, 1983b; Clay and Andersen, 1996; Veenakumari et al., 1997; Nielsen, 2000; Wetterer and O'hara, 2002; Cogni and Freitas, 2002; Dorou et al., 2002), (ii) nesting behaviour and adaptations to the mangrove environment (Cole, 1980; Nielsen, 1997a,b; Dejean et al., 2003; Nielsen et al., 2003a,b; Nielsen et al., 2006), (iii) ant community interactions (territoriality) (Cole, 1983a,b; Adams, 1994) and (iv) ant–plant interactions (Johnstone, 1985; Ozaki et al., 2000; Cogni and Freitas, 2002; Cogni et al., 2003; Dejean et al., 2003; Offenberg et al., 2004a,b; Offenberg et al., 2005, 2006a,b; Offenberg, 2007). A first approach to test for ant–plant protection is to artificially apply arthropod prey on plants and check for ant predation. Cogni and Freitas (2002) investigated the ant fauna

on extrafloral nectary bearing *Hibiscus pernambucensis* Arruda in a mangrove in Brazil and found that out of 19 ant species 8 species attacked live termite baits. Similarly Cogni et al. (2003) found that 60% of artificial termite baits were detected by ants within 60 min on *H. pernambucensis* and on neighboring vegetation without extrafloral nectaries, in the same mangrove forest; this despite a higher ant occupancy frequency and mean number of ants on *H. pernambucensis* compared to the nearby plants. Attacked termites were detected after only 4 min on average. A second approach is to test if ants reduce present herbivore populations and if a reduction translates into reduced herbivory. Ozaki et al. (2000) provided compelling evidence of the reduction of a scale pest population (*Aulacaspis marina* Takagi and Williams) on *R. mucronata* by the ants *Monomorium floricola* (Jerdon) and *Paratrechina* sp. in a mangrove in Bali. On ant excluded saplings 90% of artificially introduced female scales survived a three day experiment while only 22% survived on plants foraged by ants. Offenberg et al. (2005) also found a significant reduction in the herbivore community on ant (*Oecophylla smaragdina* Fabr.) visited young *R. mucronata* trees compared to control trees without ants in a Thai mangrove. In contrast, the beneficial predatory arthropod guild was not significantly affected. In this case it was seen that the reduction in herbivore numbers resulted in significantly reduced herbivory levels on ant-trees caused by all the four major herbivores (Fig. 1 and Table 1).

A similar result was found on mature trees in the same area; ant associated trees experienced more than four times less foliovory than trees without ants, despite an overall damage of less than 3% leaf area loss. Also, damage levels within ant-trees were seen to be negatively correlated with ant densities (Offenberg et al., 2004a). The first published study on mangrove ant–plant interactions by Johnstone (1985) similarly found a trend for less foliovory on mangroves with *O.*

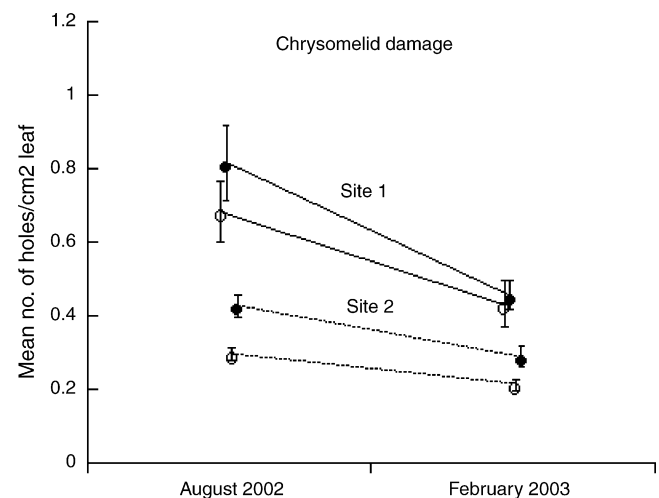Fig. 1. The amount of damage caused by chrysomelid beetles on *R. mucronata* trees with and without *O. smaragdina* ants. Symbols show the tree mean no. of holes per cm^2 leaf area on ant (open symbols) and control trees (solid symbols) at site 1 (solid lines) and 2 (broken lines) at two surveys. At site 1, N_{ants} = 7 and $N_{control}$ = 8 trees; at site 2, N = 13 trees in both groups. From Offenberg et al. (2005).

Table 1
Damage caused by three herbivores on *Rhizophora mucronata* trees with and without *Oecophylla smaragdina* ants

	Damage				Unit
	Ants		Control		
	Mean ± S.E.	N (trees)	Mean ± S.E.	N (trees)	
Tortricid	1.93 ± 1.07	20	10.01 ± 3.98	21	% Attacked shoots
Geometrid	0.40 ± 0.15	13	3.28 ± 1.43	13	% Leaves eaten
Sesarmid	0.25 ± 0.08	13	0.44 ± 0.12	13	% Eaten leaf area

Modified from Offenberg et al. (2005).

smaragdina ants on the Papuan coast, however, the difference between ant-trees and non-ant trees was not significant, leading Johnstone to conclude that ants were unable to protect mangroves. The insignificance, though, could have been caused by the pooling of leaves from different tree species. Hence, mangrove ants can reduce herbivore numbers and herbivore damage, however, reports on their effect on plant performance is scarce. One study have addressed this problem and found that ant associated trees with fewer herbivores and less folivory showed a marginally insignificant trend toward lower performance than control trees (Offenberg et al., 2005). Thus, reduced herbivory may not necessarily lead to increased plant performance since plants may compensate or even overcompensate in response to herbivory (Huhta et al., 2003). The positive effect by ants acting on the herbivore population and the herbivore damage level may also be counteracted by the indirect negative effects that ants may exert on their host plants via trophobiosis with herbivorous honeydew producing hemiptera and lycaenid larvae (Buckley, 1987) and via their nest building. In most cases, though, these effects are considered less significant than the positive effects from ants. For example, leaf nest building by *O. smaragdina* on *R. mucronata* reduced the longevity of the leaves used in the nest, but this effect was estimated to be 3–20-fold lower than the positive effect afforded via protection against foliovory (Offenberg et al., 2006b). Still lacking from this estimate, however, is the effect of sap sucking scale insects attended by the ants on these trees. At present, probably the best evidence of a positive effect by ants on plant performance is the study by Ozaki et al. (2000) which might have shown a considerable positive effect on plant survival if it had addressed this issue by prolonging the study period. Saplings in plantations with no ants experienced scale insect infestation levels (>200 females/ leaf) resulting in the death of seedlings within 5 months with up to 70% mortality, whereas nearby natural mangroves with ants had almost no scale insects.

3. Crabs

3.1. Damage by herbivorous crabs

Although the vast majority of leaf-feeding crabs actually depends on leaf litter, some species colonising both New world and Indo-Pacific mangroves evolved a tree-climbing inhabit often coupled with an herbivorous feeding regime (Fratini et al., 2005). Among these climbers, one of the most studied is surely the sesarmid crab *Aratus pisonii*, in fact, is common in mangroves colonising both the Pacific and Atlantic tropical and sub-tropical coasts of the American continent and it is known to inhabit the mangrove canopy as adult and to rely mainly on fresh leaves (Warner, 1967; Beever et al., 1979; Erickson et al., 2003). *A. pisonii* removes the top layers of the leaves by scraping the leaf surface and, although its damage does not penetrate the entire leaf, can remove up to 30% of an individual leaf (Erickson et al., 2003). In Florida, the heavy impact due to the herbivory of this tree-climber within the stands dominated by *R. mangle* has been shown by Erickson et al. (2003), which observed that the percentage of damaged leaves can be up to 30–40% of the total leaves on the trees.

Even though the species diversity of tree-climbing crabs in the Indo-Pacific systems is undoubtedly high, comprising species belonging to at least two families and five genera (Fratini et al., 2005), reliable data on the impacts of their herbivorous habits are available only for *Parasesarma leptosoma*, a mangrove-climber colonising the whole East African coasts, from Kenya to South Africa (Vannini and Ruwa, 1994; Emmerson et al., 2003). In Kenya their average density can be about 200–300 crabs per mature *R. mucronata* tree, their preferred food source, and they can damage, by scraping the leaf-tissues with their claws, up to 50–60% of the fresh leaves of the canopies (Cannicci et al., 1996a,b). Since the damages operated by crabs feeding on fresh leaves are similar to the ones due to many herbivorous insects, their implications in terms of costs for the trees should be similar, but no experimental data exists on this topic and further work is indeed required to understand the scale of crab herbivory impact and the actual defences evolved by the plants themselves.

3.2. Retention of primary productivity within the ecosystem

Crabs are known to be the main agents responsible for the high leaf litter turnover rates in mangrove systems (Lee, 1998, 2008). Sesarmids are surely the main consumers of mangrove leaf litter along the Indo-Pacific region, but their influence is highly variable, thus broad generalizations about the extent of their impacts are difficult to draw (Table 2).

Although the role of sesarmid crabs in the leaf turnover of neotropical mangroves was never considered of primary importance, with the exception of the tree-climber *A. pisonii* (Beever et al., 1979) recent studies showed how this role of litter consumption is played by the ocypodid crabs of the genus *Ucides* (Table 2). Indeed, Twilley et al. (1997) pointed out that

Table 2
Mangrove litter consumption rates, as percentage of leaf litter production, recorded for mangrove crabs belonging to Neotropic and Indo-Pacific ecosystems

Region	Mangrove	Consumption rate (%)	Crabs	Crab family	Reference
Neotropic	*Rhizophora* sp.	81	*Ucides cordatus*	Ocypodidae	Nordhaus et al., 2006
Indo-Pacific	*Rhizophora* sp.	9	*Perisesarma (Chiromates) onychophorum, P. eumolpe*	Sesarmidae	Leh and Sasekumar (1985)
		>100	*Neoepisesarma* spp., *Perisesarma (Chiromantes)* spp.	Sesarmidae	Poovachiranon and Tantichodok (1991)
		28	*Perisesarma messa*	Sesarmidae	Robertson (1986)
	Ceriops sp.	71	*Perisesarma messa, Neosarmatium smithi*	Sesarmidae	Robertson and Daniel (1989)
	Bruguiera sp.	79	*Perisesarma messa, Neosarmatium fourmanoiri*	Sesarmidae	Robertson and Daniel (1989)
	Avicennia sp.	33	*Neosarmatium fourmanoiri, Parasesarma moluccensis*	Sesarmidae	Robertson and Daniel (1989)
		44	*Neosarmatium meinerti*	Sesarmidae	Emmerson and McGwynne (1992)
		>100	*Neosarmatium meinerti*	Sesarmidae	Olafsson et al. (2002)
	Kandelia sp.	57	*Perisesarma bidens, Parasesarma affinis*	Sesarmidae	Lee (1989)

Ucides occidentalis Ortmann leaf-burying behaviour affected the litter dynamics of Ecuadorian mangroves similarly to the high rates of leaf-burrowing known for Indo-Pacific sesarmids.

On the other hand, Indo-Pacific Ocypodidae are among the main consumers of another source of organic compounds, derived from microalgal and bacterial primary production. Crabs belonging to the genera *Uca* and *Dotilla* are known to ingest benthic, as well as periphytic (Hootsmans et al., 1993), bacteria and microalgae (France, 1998; Bouillon et al., 2002a), and proved capable of removing high rates of chlorophyll *a* and bacteria near the sediment (Kristensen and Alongi, 2006).

If the role of mangrove litter retention by crabs in maintaining the organic matter into the system is certain, their trophic role is still a matter of debate (see also Kristensen et al., 2008). Do they primarily consume the leaves they store in their burrows? Freshly senescent leaves of all mangrove species, i.e. what is commonly available for the crabs, are characterised by very low nutritional values, have a very high C/N ratio, up to 100, and high concentration of tannins, which interfere with protein digestion acting as feeding deterrents. Apart from these biochemical considerations, direct observations on feeding behaviour of Indo-pacific sesarmids (Kwok, 1999; Skov and Hartnoll, 2002) and studies comparing the stable isotope signature of mangrove leaves and sesarmid crabs (Bouillon et al., 2002a,b; Thongtham and Kristensen, 2005) show that they do not totally rely on leaf litter as a food source. These recent results lead to another unresolved question, what are the other sources of food for crabs?

3.3. Enrichment of mangrove organic production

Although crabs act as the major initial processors of mangrove leaf organic matter, their trophic dependence on this matter is probably less significant than is suggested by the data on removal. Although sesarmids and ocypodids can consume up to ∼100% of the mangrove leaf litter of Old and New world mangroves, respectively, little is known about the fate of the organic matter they consume. Crabs' assimilation rate of the leaf litter is generally low (<50%), and about 60% of the dry mass of the material consumed is egested as faecal matter (Lee, 1993), resulting in high faecal rate production by crabs. As an example, Lee (1997) showed that *Perisesarma messa* Campbell, feeding on *R. stylosa* leafs in Australia, produced faecal material at a rate equivalent to about 24% of the leaf litter fall of the forest.

The physical and chemical conditions of mangrove leaf litter can change noticeably during the digestion process of crabs, and these changes can enhance the nutritional qualities of crabs faecal material, which is thus exploited by both small autochthonous and alloctonous benthic invertebrate consumers. In fact, Lee (1997) showed that *P. messa* faeces, at least 2 weeks old, were significantly richer in nitrogen, and less rich in tannins than unprocessed mangrove litter. As a result of these chemical changes, in laboratory experiments, the same faecal material proved to be a source of food of better quality than the mangrove litter for the benthic amphipod *Parhyallela* sp., attaining significantly higher mortality rates. More recently, Werry and Lee (2005) showed that mangrove organic matter is shredded to microscopic fragments of ∼200 μm in size in the faeces of *Parasesarma erythrodactyla* (Greenwood and Fielder). The faecal matter was colonised by bacteria, which proved to be ∼70× more abundant than on whole leaf litter undergoing normal decomposition. Moreover, a rise in nitrogen content that was associated with bacterial density, showed that the passage thorough the gut of the crabs can enrich the raw mangrove organic matter. Similar figures were obtained by Nordhaus and Wolff (2007) studying the feeding ecology of the Ocypodid *U. cordatus* in Brasil. They found that *U. cordatus* produces finely fragmented faecal material enriched in C, N and bacterial biomass compared to the sediment, concluding that the decomposition of mangrove leaf litter was greatly enhanced due to litter ingestion by this crab.

By transporting and processing a large amount of leaf litter and by acting as shredders, mangrove crabs thus propel a rapid enrichment of the primary production of mangroves (Lee, 1997).

3.4. Reduced competition among saplings by propagule predation

Propagule recruitment supports natural regeneration of mangrove forests and contributes to the restocking of vegetated stands, determining in the long term the structure and functioning of mangrove ecosystems. Thus, seed, seedling and propagule predation, mainly exerted by crabs, has been considered an important factor determining seedling distribution patterns in many mangrove stands as well as in terrestrial coastal forests (Green et al., 1997; Sherman, 2002; Lindquist and Carroll, 2004).

About mangrove forests, at least three models have been proposed to quantify and explain the impact of crab propagule predation on vegetation structure. The dominance–predation model suggests an inverse relationship between the rate of predation of a certain species and its dominance in the forest canopy (Smith, 1987), while the canopy-gap mediated model (Osborne and Smith, 1990; Clarke and Kerrigan, 2002) hypothesizes that predation could be more intense under closed canopies than in adjacent relatively large gaps. A third model, the so called flooding regime model (Osborne and Smith, 1990; Clarke and Myerscough, 1993) considers the time available for semi-terrestrial crabs to forage due to differential exposure to air of low intertidal and upper intertidal belts, suggesting that propagule predation may be related to inundation time, i.e. predation is lower in the lower intertidal.

The dominance–predation model was tested along the Australian north coast (McGuinness, 1997; 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 model (Smith et al., 1989), whereas many studies offered alternative explanations (for example McKee, 1995; McGuinness, 1997; Dahdouh-Guebas et al., 1998; Sousa and Mitchell, 1999; Clarke and Kerrigan, 2002).

The canopy-gap mediated model postulates a more intense propagule removal in more vegetated areas, leading to negative impacts on forest regeneration and a regulating effect, exerted by reduced competition in high density stands. Recent findings that already established propagules and saplings are fed upon less than stranded ones (Dahdouh-Guebas et al., 1997; Clarke and Kerrigan, 2002) suggest that crabs can clear high density stands and thus "help" the already established saplings to grow better. Following this frame of hypotheses, Bosire et al. (2005) suggested a possible 'mutual relationship' between sesarmid crabs and mangroves, in which mangroves provide food and a suitable habitat for the crabs, which, among other roles, reduce competition through propagule predation.

The flooding regime model was challenged as well, when Sousa and Mitchell (1999) found predation to be more intense in the lower intertidal of their study area, and showed that this differential pressure was due to a greater abundance of herbivorous crabs there than in the upper intertidal, which was dominated by *Uca* spp. The temporal relationship between lagoon water level and predation intensity on specific locations has also been established experimentally by Dahdouh-Guebas (2001) and a similar model has been proposed (Fig. 2). Dahdouh-Guebas (2001) proposed a spatio-temporal biocomplexity hypothesis that explains the role of propagule predators in the shaping of vegetation structure, and how local hydrography and anthropogenic effects may influence the apparently natural process of propagule predation. Rather than the influence of many biotic and abiotic factors on a given location, it seemed to be a chain of events (i.e. spatio-temporally separated influences of one or more biotic and abiotic factors) that leads to a particular mangrove vegetation structure or zonation (Fig. 2).

3.5. Bioturbation and consequent ecosystem engineering

Although the substantial impact of crabs bioturbating activities was well known for other coastal habitats (see for example Montague, 1980; Bertness, 1985), Smith et al. (1991) were the first to use manipulative experiments to demonstrate that sesarmid crabs are crucial mangrove ecosystem engineers. Crab bioturbation significantly decreased ammonium and sulphide concentrations in mangrove soil, thus positively benefiting mangrove productivity. Recently, other studies have also examined the role of crabs in mangrove sediment biogeochemistry. Nielsen et al. (2003a,b) observed that burrows of fiddler crabs, genus *Uca*, and roots of *Rhizophora apiculata* BL. cause iron reduction to occur down to 7 cm depth.

These findings were confirmed by Kristensen and Alongi (2006) with mesocosm experiments. These authors proved that the activities of *Uca vocans vocans* (L.) affected redox sensitive elements, such as Fe and S, down to a depth of 2 cm, even if the feeding activity of these fiddler crabs was confined to the upper few millimetres of the sediment. Kristensen and Alongi (2006) hypothesised that higher content of oxidized compound forms in the upper 2 cm was caused by continuous mixing and oxidation of surface sediment due to the activity of the crabs. Interestingly, the authors suggest that mixing can occur not only during feeding but also during other activities involving movement, such as walking when the legs sink into the sediment. Also the deposition of feeding pellets and burrowing and burrow maintenance activities probably augments the effective mixing depth, resulting in a higher growth, in terms of leaves and pneumatophores, of *Avicennia marina* saplings associated with fiddler crabs (Kristensen and Alongi, 2006; Kristensen, 2008).

Crab burrows also play an important role in affecting the groundwater flow in, and the chemistry of, otherwise compact mangrove sediments (Wolanski et al., 1992), providing an efficient mechanism for exchanging water between the swamp soil and the overlying water (Ridd, 1996), and thus resulting, among other benefits, in the removal of accumulated salt from around mangrove roots (Stieglitz et al., 2000). Increased pore water exchange, caused by crabs digging activity, may result in faster removal of phytotoxins (Howes and Goehringer, 1994).

Fig. 2. The spatio-temporal biocomplexity model (Dahdouh-Guebas, 2001) indicates that when the water level is low (or during dry seasons in mangrove forests with little tidal influence) propagules fall on the soil and may plant themselves or strand (planting and stranding strategy of Van Speybroeck, 1992), the latter of which are known to be predated more than the former (Dahdouh-Guebas et al., 1997). However, the microtopographical conditions in some forests provide more possibilities to strand, increasing the exposure of propagules to predators, which in turn are very mobile and forage considerably at low water levels (Dahdouh-Guebas, 2001). When the water level is high (or during wet seasons in mangrove forests with little tidal influence), the forest is often permanently flooded for a period, and the propagules that fall under those conditions drift away through the water. They are much less likely to be affected by propagule predators, which at that time are stuck on the mangrove roots (Dahdouh-Guebas, 2001). Once the water table decreases again and propagules can establish, propagule predators further control this establishment (establishment driver). However, considering that mature propagules are less affected by propagule predators than freshly gathered ones (Dahdouh-Guebas et al., 1997), and considering that a mature stage can be reached during the dispersal period, the propagule predation that occurs when the water table decreases is likely to be less intensive. Following establishment of a propagule, various environmental conditions (filled black arrows = proximate causes) drive survival or death of the propagule (see superscript legend below). Some of these environmental drivers are most pronounced, stressing and determining for the propagule's survival during the dry season (open white arrows = ultimate causes). It seems that the forest patch structure may be the result of the differences in environmental drivers such as salinity during the dry season (development driver), but that the dispersion of propagules to lead to any vegetation structure or zonation in the first place, is controlled by the wet season (dispersion driver). Therefore, rather than the influence of many biotic and abiotic factors on a given location, it seems to be a chain of events (i.e. spatio-temporally separated influences of one or more biotic and abiotic factors) that leads to a particular mangrove vegetation structure or zonation. Superscripts indicate the following papers from the Aquatic Botany Special Issue on Mangrove Ecology dealing with these topics: (1) Nagelkerken et al. (2008), (2) Di Nitto et al. (in press), (3) Gilman et al. (2008), (4) Kristensen et al. (2008), (5) Krauss et al. (2008), (6) Komiyama et al. (2008), (7) Walters et al. (2008) and (8) Berger et al. (2008). Dark grey arrows indicate the logical sequence of events, whereas black and white arrows indicate causes or influences from. Influences exerted entirely or in part by fauna are typed in italic Arial font; the others are abiotic. The light grey arrow roughly indicates the flow of the cycle. The inset photograph shows six individuals of *Neosarmatium meinerti* struggling to conquer a *Rhizophora mucronata* propagule.

4. Molluscs and other marine taxa

4.1. Gastropods

Together with decapod crustaceans, molluscs are the most well represented taxon of marine origin in mangrove forests (Plaziat, 1984; Kathiresan and Bingham, 2001). The high mangrove mollusc diversity is probably determined by the availability of a diverse range of microhabitats (see Plaziat, 1984). In mangroves, molluscs occupy all the levels of the food web, as predators, herbivores, detritivores and filter feeders. They are zoned both horizontally (i.e. along the sea-land axis) and vertically (i.e. at diverse heights from the ground) and include both mobile and sessile species. Despite this, the overall ecological role of molluscs' and the effects they exert within the mangrove ecosystem is far from clear.

In the Indo-Pacific mangals, adults of *Terebralia palustris* Herbst (Gastropoda; Potamidae) are the only herbivorous molluscs, and for both their large size (they can reach a shell length of 16 cm, Houbrick, 1991) and their remarkable densities (among the most impressive values, Plaziat, 1984, reported 150 adults m^{-2} in New Caledonia), they are protagonists in fallen leaf consumption and degradation (Slim et al., 1997; Fratini et al., 2004). These mud whelks consume significant amounts of fallen leaves: Fratini et al. (2004) demonstrated that in a Kenyan mangrove during a single low tide, if fed ad libitum, the mud whelk population alone was able to consume about five times the daily *R. mucronata* leaf production. Moreover, *T. palustris* leaf consumption is not restricted to low tide, since this species eats at high tides too (Fratini et al., 2004) chemically locating the fallen leaves underwater. For this reason, snails are able to entrap additional primary production before it is removed by ebbing currents.

T. palustris also consumes propagules of *A. marina* and Rhizophoracea, and thus it influences mangrove restoration and regeneration (Plaziat, 1984; Dahdouh-Guebas et al., 1998;

Dahdouh-Guebas, 2001; Fratini et al., 2004; Bosire et al., 2008). The damage occurs due to the radula of adult mud whelks, and in Sri Lanka at least, it was observed that this gastropod prefers consuming the epicotyl of mangrove propagules, as opposed to crabs which feed on the hypocotyls (Dahdouh-Guebas, 2001).

Another important effect exerted by large mobile gastropods is the destabilization of the sediment due to the tracks left by their heavy shells. Carlen and Ólafsson (2002) experimentally demonstrated that the presence of adult individuals of *T. palustris* induces mud surface rearrangement, affecting the abundance of meiofauna community (decreasing density) and of the cyanobacteria carpet (complete disappearance). Overall, this induces a general modification of the biological, chemical and physical parameters of the mangrove soil surface (Carlen and Ólafsson, 2002).

4.2. Fouling communities on roots and trunks: sponges, oysters and barnacles

Mangrove roots and trunks represent zones of hard substrate colonised by fouling organisms, the dominant group of which is represented by the massive sponges (Porifera) that exert direct and indirect effects on mangrove plants. First, they increase plant growth by inducing the formation of adventitious rootlets that are able to absorb ammonium and other nitrogenous compounds produced by the sponges themselves and to transfer this ammonium into cable roots (Ellison et al., 1996). It has been demonstrated that this mechanism may increase mangrove nitrogen uptake by about 10% (Ellison et al., 1996), significant where it is often limiting. Second, due to their physical structure, sponges (as well as ascidians) protect mangrove roots from attack by wood boring isopods (Ellison and Farnsworth, 1990). By removing sponges from mangrove roots Ellison and Farnsworth (1990) estimated a 55% decrease in root growth due to isopod burrowing activity. Finally, the relation between mangroves and root-fouling sponges appears a facultative mutualism since mangrove roots are the only hard substrata available for these epibiontic organisms and they passively leak carbon to sponges tissues (Ellison et al., 1996).

Oysters and barnacles also foul mangrove roots and trunks (Pinto and Wignarajah, 1980; Ross and Underwood, 1997). The epibenthic fauna includes primary and secondary consumers, and its impact on mangrove trees is considerable: barnacle assemblage can negatively affect root growth (Perry, 1988) and heavy oyster cover can damage or break prop roots (Ellison and Farnsworth, 2001). In many mangrove forests world-wide, oysters are consumed by local people, and the breakage of the aerial roots where this mollusc grows is a consequence of oyster harvests (Pinto and Wignarajah, 1980).

4.3. Isopods

The cosmopolitan wood boring isopod *Sphaeroma terebrans* Bate (Isopoda; Sphaeromatidae) bores into the aerial roots of the fringing zone. The impact of isopod burrowing has not been definitively clarified. As a result of isopod injuries, on one hand,

some documented a negative impact, due to reduction in root growth (Rehm and Humm, 1973; Perry, 1988; Ellison and Farnsworth, 1990,1992) or to the energetic costs of repairing damage (Brooks and Bell, 2002). On the other hand, Simberloff et al. (1978) demonstrated a positive effect, showing that isopod boring enhances mangrove prop root production. In East-Africa, this organism has been shown to shape mangrove tree distribution (Svavarsson et al., 2002). It therefore seems that isopods, as decapods and gastropods, are active ecological engineers in mangroves.

5. Vertebrates

From the point of view of influence on tree development and regeneration of mangroves, vertebrates are probably the least documented. A variety of fish, reptiles, birds and mammals have been observed in mangroves (Field, 1995; Stafford-Deitsch, 1996; Mastaller, 1997), but few in-depth studies exist on them. Hippopotami frequent the mangals of South Africa, and crocodiles occur in many mangrove areas throughout Australasia, Africa and Latin America (loc. cit.). Proboscis monkeys eat mangrove leaves in Borneo (Meijaard and Nijman, 2000; Verhaegen et al., 2002), deer forage on shoots in the mangals of the Sundarbans and the Florida Keys (Siddiqi and Husain, 1994; Siddiqi, 1995; Lopez et al., 2004; Barrett and Stiling, 2006) and some primates consume oysters present on mangrove roots inducing their mechanical damage or breakage (Fernandes, 1991). In Australia, sea turtles have been reported to feed on fruiting *Avicennia* propagules hanging close to the water surface (Duke, 2006). In India, one of the few studies investigating the interaction between large mammals and mangrove plants reported compensatory regrowth in *Avicennia* resulting from browsing by feral water buffaloes (Dahdouh-Guebas et al., 2006; Rist and Dahdouh-Guebas, 2006). Vegetation trampling is probably an effect from domestic cattle, but experimental studies investigating this in-depth are missing (loc. cit.). Birds and bats are known to pollinate mangrove representatives of the genus *Sonneratia* (Tomlinson, 1986; Coupland et al., 2006), while the hummingbird *Amazilia tzacatl* De la Llave is the sole pollinator of *Pelliciera rhizophorae* Triana and Planch in Central America (Prahl, 1987). Onuf et al. (1977) demonstrated that birds nesting in mangrove stands are a significant source of inorganic nitrogen for *Rhizophora* trees.

6. Conclusions

Recent acquisitions, missing pieces and open questions in the mangrove ecology puzzle.

6.1. Recent acquisitions: the impact of ocypodid crabs and gastropods

As pointed out in a number of reviews on mangrove crabs (Jones, 1984; Lee, 1998; Kathiresan and Bingham, 2001), the understanding of the strong impact of Indo-Pacific sesarmid crabs represented a real paradigm shift in mangrove ecology.

Their most ascertained ecological roles include, amongst others, retention of forest products, processing of organic matter, determination of mangrove community structure by means of differential consumption of propagules, changes in particle size distribution coupled with enhanced soil aeration (Jones, 1984; Lee, 1998).

Although Sesarmidae are still considered one of the most important taxa in shaping mangrove structure and functioning, recent literature emphasizes that other marine invertebrates can have tremendous impacts on mangrove systems. The Ocypodidae of the genus *Ucides* have a heavy impact in terms of retention of forest products and processing of organic matter on New world mangroves (Twilley et al., 1997; Nordhaus et al., 2006). Ocypodid crabs have been shown to not only have the same role of Sesarmidae, where these latter crabs are less abundant, but also to have a similar degree of impact, consuming up to 81% of the total litter production (Nordhaus et al., 2006). Moreover, other Ocypodidae, the fiddler crabs (genus *Uca*), abundant in both New and Old world mangroves, process large amounts of primary production in terms of microalgae, contributing consistently in retention of mangrove production (Jones, 1984). These small, but very abundant crabs are now considered ecosystem engineers, able to change the particle size distribution and to enhance soil aeration and mangrove primary production (Nielsen et al., 2003a,b; Kristensen and Alongi, 2006; Kristensen, 2008).

6.2. Missing pieces: ant–plant interactions

Given that ants are among the most abundant insects in mangrove ecosystems, ant–plant interactions may form an important contribution to our understanding of insect–plant dynamics in these habitats. Little attention has been devoted to mangrove ant ecology but the few studies that have addressed ant–plant interactions almost unequivocally support the idea that ants are able to provide some degree of protection against herbivore communities and the damage they inflict, including relieving mangroves from important herbivore groups such as scale insects (Diaspididae; Ozaki et al., 2000), lepidopteran larvae (Pyralidae and Geometridae; Offenberg et al., 2005), leaf beetles (Chrysomelidae; Offenberg et al., 2004a,b; Offenberg et al., 2005) and even from sesarmid male crab grazing via an indirect interaction (Offenberg et al., 2006a). Furthermore, in terrestrial agroecosystems, identical ant species are known to protect a range of crops against more than 40 different herbivores (Way and Khoo, 1992; Peng and Christian, 2004) and a multitude of empirical studies on ant–plant interactions in natural habitats support the wide distribution of ant–plant protection mutualisms (Bronstein, 1998). Hence, in terrestrial habitats ants are able to increase plant fitness. In mangrove forests there is at present, no evidence that protection against herbivore damage translates into increased plant performance affecting forest structure. This could be the focus of future mangrove ant–plant studies. It seems unlikely that ants should not have any positive effects on mangrove performance.

6.3. Open question: is herbivory by insects and crabs a positive or a negative impact?

While herbivory is usually considered to be a negative impact, this view is not straight forward and its dominance in the literature may reflect that negative impacts are more readily apparent and more readily measured than potentially positive feedbacks and energy transfers.

While the effect of insect herbivore activities may negatively impact upon certain aspects of an individual tree performance and vigour, the effect may be positive on overall ecosystem performance, for example where the loss of leaf material from a tree returns nutrients to the ecosystem, rather than having them locked up within the trees. Burrows (2003) and Feller (2002) showed that the feeding activities of leaf-feeding and wood-boring insect herbivores, respectively, altered the quality and quantity of mangrove litterfall by premature loss of younger leaves that have a higher nutrient content. The significant light gaps created by branch death resulting from the feeding activities of wood-borers (Feller, 2002) may also provide opportunities for seedling colonisation and alteration to forest structure. In essence, the true ecological role played by insect herbivores is not just confined to mere assessments of the amount of tissue lost or damaged but has its effects at the scale of whole plant performance and ecosystem functioning. Future studies of mangrove herbivory will need to be cognisant of examining the true role of insects in the ecosystem, rather than just extrapolating judgements from assessments of the amount of plant material consumed.

The same conclusions can be drafted about crab herbivory and, in particular, about their feeding on propagules. Although the negative impact of propagule removal on newly replanted stands has been identified as one of the major causes of unsuccessful reafforestation attempts, nevertheless, it remains clear that crabs can also positively influence natural mangrove regeneration (see also Steele et al., 1999; Clarke and Kerrigan, 2002; Bosire et al., 2005). Saturation of predators by shedding hundreds of propagules at once (Dahdouh-Guebas et al., 1997), or changes in palatability over time (loc. cit), which can be linked to dispersal period (Fig. 2), were suggested as possible adaptations by mangroves to propagule predation, but in-depth experimental research is lacking.

Further research in the direction of propagule removal in closed canopies/high density reforested plantations and rehabilitated stands may provide evidence of a positive impact on sapling competition for space and useful ecological information critical in the management of mangrove stands. This further research should include assessment of the indirect influence of propagule removal on other potential regeneration constraints and, ultimately, on the vegetation dynamics in reforested plantations.

At present, our conclusions are that recent work on mangrove macrobenthic impacts put new actors on the stage, for instance ocypodid crabs, ants and gastropods, revealing that the well known effects of propagule predation by sesarmid crabs and herbivory by insects are only parts of the complex faunal impact on mangrove systems. We should emphasize that,

although invertebrates have strong impacts on mangrove trees, their biodiversity has a prominent role in controlling key aspects of mangrove systems, such as their biogeochemical and ecological functions (cf. Bouillon et al., 2008) and, eventually on the whole ecosystem functioning (sensu Field et al., 1998). Hence, both ecological studies and management of mangroves should be done with benthic biodiversity in mind (Duke et al., 2007; Ellison, 2008).

Acknowledgements

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