Impacts of Disturbances on Species Specific Interactions between Crabs and Plants in Mangrove Ecosystems

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Chapter 1

General Introduction

1. What are mangrove forests and what ecosystem functions and services do they provide?

Mangroves are trees or shrubs that grow in intertidal forests situated in the coastal area or in estuaries (Duke et al. 1998, Nagelkerken et al. 2008). There are about 70 mangrove species belonging to 27 genera from 20 families and 9 orders. Mangrove forests occupy 181 000 $km^2$of the world tropical coastal area (Alongi 2008) and provide essential functions and services for the coastal populations (Spalding et al. 2014). Mangrove species diversity is high in the West Indo Pacific region and low in Atlantic east pacific. Brazil, Australia, Indonesia and Nigeria all together cover almost 43% of the world mangrove forest (Alongi 2002).

Mangrove forests are frequently inundated by the tides of salty or brackish water. To deal with those stressful conditions, mangrove plant species have special anatomical and physiological adaptations in their roots, trunks, leaves and fruits. For instance, mangrove trunks are supported by specific root systems to sustain themselves in muddy soft and often anoxic sediments. Some mangrove species develop salt glands or salt hairs in their leaves to sequester salt, while other mangrove species exclude the salt by ultra-filtration in their xylem (Takemura et al. 2000, Parida et al. 2004). Mangrove species usually have floating seeds that already progress as a living individual plant, known as propagules, before leaving their parent trees to be able to successfully disperse and recruit in that harsh environment.

Through their extensive spatial distribution and their specific attributes, mangrove forests play important roles including protecting shorelines against wind, wave energy and tsunamis (Alongi 2008), supporting coastal fisheries by providing habitat for nursery and feeding ground (Walters et al. 2008), offering a safe haven for birds and seabirds, supplying timber for constructions and charcoals, and offering chemicals for medicinal products. The mangrove forests provide these functions and services thanks to the high productivity of mangrove trees and mangrove understory species, which are the main primary producers of the above ground compartment of mangrove ecosystem. For instance, the high mangrove trees break the wind, while their extensive root systems aid protection against waves. Likewise, the stilt roots of mangrove trees provide a habitat for fish, whereas their branches and stems can be used as nesting place for birds.

2. The importance of species specific interactions between crabs-mangrove plants for mangrove ecosystem

In addition to mangrove trees and understory species, another important component of the mangrove environment (in terms of impacts on ecosystem functioning and the provision of ecosystem services) is formed by the fauna species that live between the roots of the mangrove plant species. Of all mangrove fauna species, mangrove crabs may be the most pronounced given their omnipresence. Crabs play a significant role in mangrove ecosystems. For instance, crabs decompose litter and recycle mangrove primary production with the help of the soil microbial community. The nutrients thus transformed and released are again available to mangrove plants. At the same time, mangrove crabs also graze on mangrove green leaves (Farnsworth and Aaron 1991) and may therefore potentially reduce mangrove primary productivity.

Some studies (Ashton 2002, Nordhaus et al. 2006, Chen and Ye 2008, Imgraben and Dittmann 2008, Thongtham et al. 2008) revealed the importance of mangrove crabs feeding on mangrove litter and brought forward new understanding on how the aboveground compartment and the belowground components of mangrove ecosystems are connected with each other. Mangrove crabs had been reported to process no less than 70% of the total mangrove leaf litter of Australian (Robertson and Daniel 1989) and African mangroves (Micheli et al. 1991). Other studies reported the susceptibility of mangrove plant species to leaf herbivory by mangrove crabs. Finally, crabs affect mangrove forest dynamics by consuming propagules (Smith III 1987). Mangrove propagule predation by crabs can significantly impact mangrove forest regeneration (McKee 1995, Dahdouh-Guebas et al. 1997, Bosire et al. 2005, Dahdouh-Guebas et al. 2011).

These crab-plant interactions do not affect all mangrove plant species to the same extents. Some of the above mentioned studies revealed that the susceptibility of mangrove leaves and propagules to crab consumption was determined by their chemical and physical properties such as C:N ratios, tannin content, propagules size and stage of leaf decomposition (Lacerda et al. 1986, Erickson et al. 2004, Nordhaus et al. 2011). Other studies (Smith III 1987, Smith III et al. 1989) suggested, however, that propagule predation was mainly determined by their abundance (and thus by the dominance of the plant species in the field), unrelated to propagule chemistry. So far, the low number of studies does not allow us to formulate general rules about mangrove crab-plants interactions since many results turn out to be idiosyncratic (Smith III et al. 1989, Boon Pei et al. 2008, Chen and Ye 2008). At the same time though, mangrove crab-plant species interactions are crucially important for the functioning of the entire ecosystem. Consequently, a significant change in one of these components can potentially alter the structure and functioning of the other component.

Many of those interactions, may –instead of being related to substrate quality or substrate availability- be species-specific. For instance, certain crab species such as *Aratus pisonii* prefer grazing on the green leaves of *Rhizophora mangle* over grazing on other species such as *Laguncularia racemosa* and *Avicennia germinans* (Erickson et al. 2003). These species-specific preferences may affect the relative abundance of different plant species. On the other hand, the susceptibility of *Rhizophora mangle* to herbivory decreased significantly in the association with *Laguncularia racemosa* and *Avicennia germinans* (Erickson et al. 2012). In addition, evidence suggests that different crab species prefer different litter species, which suggests a decoupling from litter quality (Micheli 1993b) while in addition growth and reproduction of mangrove crab species depended on the litter species it fed upon (Micheli 1993a). Understanding the specificity and the impacts of plant-crab interactions within mangrove ecosystems have been and still are a challenging area of study. Studies that investigated the specificity of the plant-crab interactions in propagule predation and whether such specificity is congruent with that of interactions with respect to litter decomposition are currently unknown. Moreover, hardly any study so far tried to understand the role of mangrove crabs in the overall nutrient recycling in mangrove ecosystems and their impacts on mangrove primary production, let alone the importance of species-specific plant-crab interactions therein.

3. Mangrove ecosystems are increasingly disturbed

Mangrove ecosystems in many parts of the world are increasingly disturbed (Valiela et al. 2001). For instance, Indonesia lost many mangrove forests in West Papua, Borneo, Sumatra and Java (Burbridge and Koesoebiono 1982). Sundarbans mangroves in India (Kathiresan and Rajendran 2005) and Bangladesh (Harun-or-Rashid et al. 2009) are also disturbed. Similarly, mangrove forests in Africa (Olagoke et al. 2013), in Belize and other parts of South America (Ellison and Farnsworth 1996) are severely disturbed. These disturbances cause habitat changes and as a consequence affect the structure of interactions between the plant and animal communities within the system (Granek and Ruttenberg 2008). Small and medium habitat changes most likely limit the impacts on these interactions only to a little extent. Systems that are impacted by such relatively small disturbances, which are often natural disturbances, will likely naturally recover (Roth 1992, Smith et al. 1994, Sherman et al. 2000, Baldwin et al. 2001). However, severe disturbances, especially anthropogenic disturbances in the form of mangrove tree cuttings will often lead to significant damage (Granek and Ruttenberg 2008). The diversity of mangrove vegetation as a result of mangrove tree cutting may decline and could potentially reduce mangrove faunal abundances. Also the plant-fauna interactions may be strongly altered and may potentially decrease the ability of the entire system to function properly up to the point in which natural recovery does not seem to be possible anymore. Moreover, major disturbances will cost the system to decrease significantly in propagules availability (Harun-or-Rashid et al. 2009), resulting in the prevalence of invasive plant species (Biswas et al. 2007). To some extent a severely disturbed system could even continuously and strongly deviate from its original undisturbed state. Whether these impacts of anthropogenic disturbance truly occur and at which conditions is, however, currently unknown but is likely dependent on the extent and direction to which the interactions between plants and fauna in mangrove ecosystems are altered. Such alterations may both directly relate to the removal of specific plant or crab species, indirectly through favoring specific plant or crab species (e.g. through dispersal limitations or reduction in propagule availability) or indirectly through affecting the environmental conditions that drive growth and survival rates of particular organisms and the expression of the interactions. Whatever mechanism occurs, since the functioning of mangrove vegetation and mangrove faunal community is so interdependent, changes in their interactions are likely to affect the entire ecosystem functioning as well as the benefits to other adjacent ecosystems.

4. The aims and hypotheses of this study

Through this study, I aim to: (1) Examine the nature of mangrove plant-crab interactions, and their impacts on the functioning of the mangrove ecosystem through nutrient recycling, and herbivory and the predation on seeds and propagules; and (2) Understand how these interactions and their impacts are affected by disturbances. While the importance of plant-crab interactions is in general understood, studies on this topic in mangrove ecosystems tend to focus on positive interactions (burrowing, litter turnover), whereas impacts may also be negative (herbivory of leaves and propagules). As a consequence, the relative importance of negative vs. positive interactions for mangrove ecosystem functioning and vegetation composition is not well understood and has never been quantified. Moreover, it is unknown to which extent the balance between negative and positive interactions on e.g. vegetation productivity depends on the species identity of the plant species and crab species involved in the light of the potential species-specific nature of the crab-plant interactions. And finally, the importance of disturbance on those interactions (both directly and indirectly through affecting the species composition and thus the species-specific nature of the interactions) is completely unknown, let alone the impacts of changes in those interactions for the stability/resilience of mangrove ecosystems upon disturbance.

Therefore, in this thesis I will examine (1) the impacts of mangrove disturbances on the biomass, species richness and species composition of mangrove plant and crab species, (2) and differentiate factors determining crab consumption on mangrove leaf litter, green leaves and tree propagules, (3) the impact of mangrove disturbances and propagule predation by crabs on tree recruitment and survival rates, and (4) the impacts of mangrove crabs on the decomposition rates of mangrove leaf litter, on green leaf herbivory and simultaneously evaluate their positive and negative impacts on mangrove productivity.

I hypothesize that (1) disturbances will reduce tree and crab species richness and abundances in mangrove ecosystems, (2) consumption of mangrove leaf litter, mangrove green leaves and propagules does not only depend on the quality of the substrate or the feeding capacity of the crab species, but will highly depend on species-specific interactions, (3) mangrove disturbances will increase limitations to tree establishment already imposed by propagule predation by crabs and reduce propagules recruitment and survival rates, and (4) crab consumption on mangrove leaf litter will increase mangrove productivity, while mangrove herbivory on green mangrove leaves will decrease mangrove productivity. In addition, we hypothesize that the balance between decomposition and herbivory impacts will depend on the species identity of both crab and plant species involved given the species-specific nature of the interactions. Together, this research also aims at (3) to gain insight in the ability of mangrove ecosystems to recover naturally following disturbances.

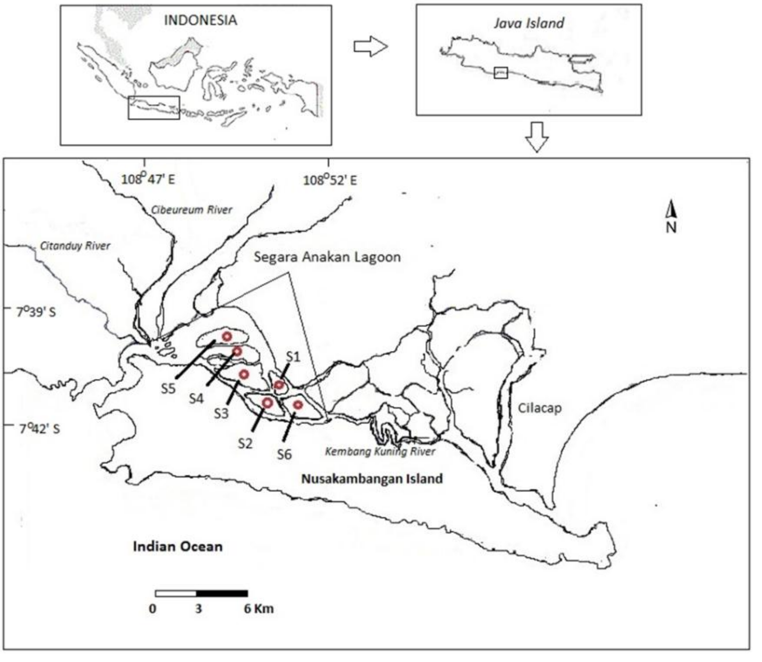

Figure 1.1. Map of Segara Anakan mangrove forest. Location of the six paired disturbed and undisturbed study sites (labeled S1, S2, S3, S4, S5 and S6) at six islets of Segara Anakan lagoon, Cilacap, Central Java, Indonesia.

5. The Segara Anakan Mangrove area as study site

I executed this study and test the hypotheses phrased in the mangrove forest of Segara Anakan, located in the Segara Anakan estuary in the South West region of Central Java (Figure 1.1). The mangrove forest of Segara Anakan grows in the formerly newly-formed lands within the Segara Anakan estuary. The formation of newly-formed lands was the result of heavy sedimentation by sediments brought by the various rivers flowing into the estuary. The sedimentation is a direct consequence of forest cutting activities in the upstream regions of these rivers. Especially the Citanduy River brings much sediments, which started back in the last century. The sedimentation continues up till now, as does the establishment of new mangrove forest.

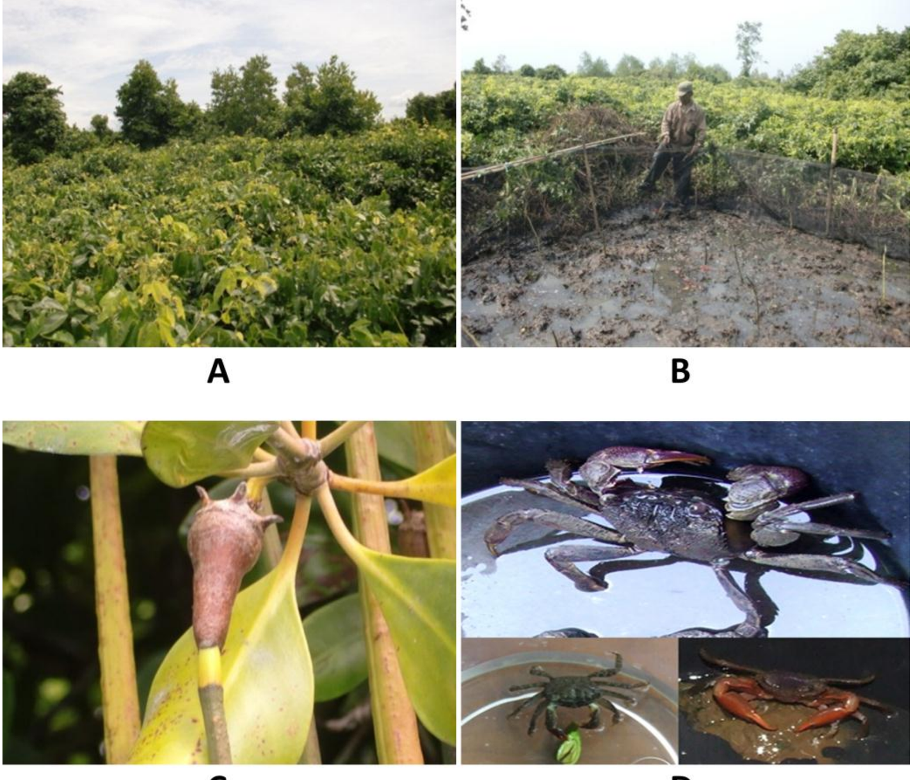

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Figure 1.2. a) Segara Anakan mangrove forest with patchy disturbed area (front) occupied by the mangrove understory species *Derris trifoliate* and *Acanthus illicifolius* and undisturbed area (back) dominated by different kinds of mangrove tree species, (b) experimental gap created for this study, (c) the mangrove species *Ceriops tagal* with abundant propagules, (d) mangrove crabs of *Episesarma versicolor, Perisesarma indiarum and Metaplax elegans*.

The Segara Anakan mangrove forest was formerly rich in mangrove vegetation and faunal community. However, during the last five decades Segara Anakan mangrove has suffered from heavy mangrove trees cutting and got severely disturbed. People cut mangrove trees and used them for house constructions and as fuel woods. In the 1980s people also cleared some parts of the mangrove forest for shrimp ponds, but now most of the shrimp ponds have gone and left a severely disturbed mangrove behind. Even though mangrove was assumed to be able to recover easily after the disturbance, this assumption does not seem to be entirely true for the Segara Anakan mangrove forest as most of the formerly disturbed mangroves are now dominated by the mangrove understory species *Derris trifoliata* and *Acanthus ilicifolius* (Figure 1.2). These species have formed a thick, almost unsurpassable, vegetation of intertwined branches. The

Segara Anakan mangrove now consists of patches of disturbed and undisturbed mangrove areas. Given the occurrence of both disturbed and undisturbed areas, and given that the disturbances prevailing in Segara Anakan are representative for disturbances as occurring elsewhere in tropical mangrove ecosystems, the Segara Anakan mangrove seems to be a proper case study to study and to evaluate our hypotheses.

6. Overview of this thesis

Following this general introduction chapter, I will first describe the results of a field survey in the Segara Anakan mangrove forest in Chapter 2. This survey was performed to examine the impact of mangrove disturbances on the community structure of crabs and plant species and to evaluate field evidence on the occurrence, expression and alterations of crab-plant links as related to disturbances. In Chapter 3, we provide a comprehensive analysis of feeding preferences of different mangrove crab species for different plant species and different plant parts of these plant species, including propagules, green leaves and leaf litter. By including crab and plant species prevailing at undisturbed and disturbed field conditions, respectively, we were able to examine species-specific crab-plant interactions through herbivory upon disturbance of mangrove ecosystems. We then tested whether these feeding preferences in relation to disturbance also occurred in the field. We executed a field experiment in which we followed the vegetation dynamics, seed rain and seedling establishment in disturbance-mediated gaps over a time period of multiple years (Chapter 4). Through this set-up, we were able to examine the ability of disturbed mangrove ecosystems to recover naturally under the pressure of propagule predation by crabs. We then performed mesocosm experiments (Chapter 5) to unravel the possible positive and negative impacts of mangrove crabs on plant biomass by comparing the net balance of crab herbivory versus nutrient release by fragmentation on mangrove biomass through crabs feeding on mangrove leaf litter while concurrently grazing on the intact green living mangrove leaves. We then discuss and integrate the results of this study in Chapter 6) to comprehensively draw lessons from what we can learn from this study.

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