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SPATIAL PATTERNS AND PROCESSES IN A REGENERATING MANGROVE FOREST

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ABSTRACT

The global effort to rehabilitate and restore destroyed mangrove forests is unable to keep up with the high mangrove deforestation rates which exceed the average pace of global deforestation by three to five times. Our knowledge of the underlying processes of mangrove forest regeneration is too limited in order to find suitable techniques for the restoration of degraded mangrove areas. The general objective of my dissertation was to improve mangrove restoration by understanding regeneration processes and local plant-plant interaction in a regenerating *Avicennia germinans* forest.

The study was conducted in a high-shore mangrove forest area on the Ajuruteua peninsula, State of Pará, Northern Brazil. The dwarf forest consisting of shrub-like trees is recovering from a stand-replacing event caused by a road construction in 1974 which interrupted the tidal inundation of the study area. Consequently, infrequent inundation and high porewater salinity limit tree growth and canopy closure.

All trees and seedlings were stem-mapped in six 20 m x 20 m plots which were located along a tree density gradient. Moreover, height, crown extent, basal stem diameter of trees were measured. The area of herbaceous ground vegetation and wood debris were mapped as well. The mapped spatial distribution of trees, seedlings and covariates was studied using point pattern analysis and point process models, such as Gibbs and Thomas point process, in order to infer underlying ecological processes, such as seed dispersal, seedling establishment, tree recruitment and tree interaction.

In the first study (chapter 2), I analyzed the influence of abiotic and biotic factors on the seedling establishment and tree recruitment of *A. germinans* during the recolonization of severely degraded mangrove sites using point process modeling. Most seedlings established adjacent to adult trees especially under their crown cover. Moreover, seedling density was higher within patches of the

herbaceous salt-marsh plants *Blutaparon portulacoides* and *Sesuvium portulacastrum* than in uncovered areas. The higher density of recruited *A. germinans* trees in herb patches indicated that ground vegetation did not negatively influence tree development of *A. germinans*. In addition, tree recruitment occurred in clusters. Coarse wood debris had no apparent effect on either life stage. These results confirm that salt-marsh vegetation acts as the starting point for mangrove recolonization and indicate that the positive interaction among trees accelerates forest regeneration.

In the second study (chapter 3), I analyzed how intraspecific interaction among *A. germinans* trees determines their growth and size under harsh environmental conditions. Interaction among a higher number of neighboring trees was positively related to the development of a focal tree. However, tree height, internode length and basal stem diameter were only positively associated in low-density forest stands (1.2 trees m^{-2}) and not in forest stands of higher tree density (2.7 trees m^{-2}). These results indicated a shift from facilitation, i.e. a positive effect of tree interaction, towards a balance between facilitation and competition.

In the third study (chapter 4), I used point process modeling and the individual-based model mesoFON to disentangle the impact of regeneration and interaction processes on the spatial distribution of seedlings and trees. In this infrequently inundated area, propagules of *A. germinans* are only dispersed at a maximum distance of 3 m from their parent tree. Furthermore, there is no evidence that the following seedling establishment is influenced by trees. I was able to differentiate positive and negative tree interactions simulated by the mangrove model mesoFON regardless of dispersal processes based on static tree size information using the mark-correlation function.

The results of this dissertation suggest that mangrove forest regeneration in degraded areas is a result of facilitative and not competitive interactions among mangrove trees, seedling and herbaceous vegetation. This has important implications for the restoration of degraded mangrove forest. Degraded mangrove areas are usually restored by planting a high number of evenly spaced seedlings. However, high costs constrain this approach to small areas. Assisting natural regeneration could be a less costly alternative. Herbaceous vegetation plays a crucial role in forest recolonization by entrapping propagules and possibly ameliorating harsh environmental conditions. So far only competition among mangrove trees has been considered during restoration. However, facilitative tree interactions could be utilized by planting seedling clusters in order to assist natural regeneration instead of planting seedlings evenly-spaced over large areas.

This dissertation also showed that point pattern analysis and point process modeling can enable forest ecologists to describe the spatial distribution of trees

as well as to infer underlying ecological processes.

Keywords: *Avicennia germinans*, Recolonization, Mangrove degradation, Facilitation, Competition, Propagule dispersal, Gibbs point process, Thomas point process, Mark correlation function, Individual-based model, mesoFON

1 GENERAL INTRODUCTION

Mangrove forests consist of trees and shrubs that grow along tropical and sub-tropical coastal regions and tolerate saline and anaerobic soil conditions (Ball, 1996; Tomlinson, 1994). Mangrove regeneration dynamics have been studied under the influence of small-scale disturbances, e.g. lightning strike, and large-scale disturbances, e.g. hurricane, clear-cut and degradation (Duke, 2001; Roth, 1992; Sherman et al., 2000). The beneficial effects of canopy gaps for the resilience of mangrove forest have been underlined (Diele et al., 2013; Kautz et al., 2011; Sherman et al., 2000; Vogt et al., 2013). However, large areas of mangrove forest have been destroyed and degraded due to infrastructure development which alters hydrological regimes and conversion for other land-uses, such as shrimp, salt and rice farming (Alongi, 2002; Primavera and Esteban, 2008). In the past four decades, 35% of the area of mangrove forests has been lost globally (Valiela et al., 2001) due to human conversions of coastal wetlands to aquaculture, agriculture and urbanization (Primavera and Esteban, 2008; Saenger, 2002). According to Giri et al. (2011) the global area of mangrove forests declined to 137,760 km² in the year 2000.

Globally an area of 150,000 ha needs to be restored every year in order to compensate the annual loss of mangrove forests (Bosire et al., 2008). However, most rehabilitation projects fail in restoring the mangrove ecosystem and providing previous environmental services (Lewis III, 2005). There are several explanations for the failure of mangrove afforestation projects. Samson and Rolon (2008) suggested that afforestation projects in the Philippines failed because the selected mangrove species was not adapted to the site conditions. Semesi and Howell (1992) observed a similar situation in Tanzania where afforestation of abandoned salt pans failed because the selected species could not cope with the high salinity and acidification. Stubbs and Saenger (2002) recommend a survey of the degree of water logging, inundation frequency and level, as well as

porewater salinity in order to select a suitable mangrove species for the local site conditions (site species matching). Gedan and Silliman (2009) argue that site species matching is just one reason for the high seedling mortality after afforestation.

Although mangroves are able to rapidly colonize large areas under favorable conditions (Proisy et al., 2009), the recolonization of degraded sites which constitute a semi-arid and hypersaline environment may be slow and isolated (Love-lock and Feller, 2003; McKee, 1995a; Milbrandt and Tinsley, 2006; Peterson and Bell, 2012). Mangrove seedlings have to be planted in degraded sites if the natural supply of propagules is insufficient due to obstructed tidal inundations (McKee et al., 2007). However, the restoration of highly degraded sites is difficult because of the extreme hydrological and physico-chemical conditions, e.g. hypersalinity and exposure to solar radiation (Alongi, 2002; Milbrandt and Tinsley, 2006). The current challenge of mangrove restoration is to provide suitable conditions in order to achieve the recovery of the forest structures and functions quickly and cost-effectively on a large scale (Bosire et al., 2003; Bosire et al., 2008; Kairo et al., 2001). Our current knowledge of the mechanisms driving the establishment and growth of mangrove tree is insufficient to develop tools for the ecological restoration of degraded mangrove forests. We can close this knowledge gap by examining the natural successional dynamics of mangroves under harsh environmental conditions.

A better understanding of natural secondary mangrove forest succession is required to develop innovative reforestation techniques. Especially, mechanisms influencing the settlement of propagules have to be investigated further (McKee et al., 2007). More information about the processes impacting propagule dispersal, propagule settlement and seedling survival are critical for assisting natural regeneration with suitable interventions (Balke et al., 2011).

Although facilitation, i.e. positive plant-plant interaction, has been identified as mechanism which influences plant survival and growth, most studies of mangrove forest development have only focused on competition and predation (Berger et al., 2006; Berger et al., 2008). Few studies analyzed facilitative interactions during mangrove secondary succession. Bosire et al. (2003) observed that non-planted mangrove species colonized plantation stands of different mangrove species more rapidly than degraded sites. Milbrandt and Tinsley (2006) and McKee et al. (2007) have proven that inter-specific facilitation takes place between herbaceous plants and mangrove recruits. Although mangrove forests form often naturally monospecific stands according to the species zonation along the gradient from sea toward land (Saenger, 2002, p. 194), studies about intraspecific facilitation between mangrove trees of the same species are

very limited (Vogt et al. 2014).

Facilitation between different life-stages, for example the sheltering of seedlings by adult plants, has been observed especially in arid ecosystems and is referred to as nurse plant effect (Tielbörger and Kadmon, 2000) or nurse plant syndrome (Callaway and Walker, 1997). Various interaction mechanisms can cause the positive effect of nurse plants. Nurse plants may ameliorate the negative impact of environmental stress factors, such as extreme temperature, reduce herbivory or enrich the soil with organic material and nutrients (Gómez-Aparicio et al., 2005a; Gómez-Aparicio et al., 2008).

Mangrove restoration has been influenced strongly by afforestation and reforestation techniques developed for terrestrial forest ecosystem. Even-spaced planting arrangements do not represent natural regeneration patterns of mangrove forests but imitate terrestrial plantation forestry (Huxham et al., 2010). The main assumption is that competition between seedlings has to be reduced by establishing evenly spaced plantations (Gedan and Silliman, 2009). In addition, the convenience of implementing regular spaced planting is another reason for its extensive use. But conventional restoration methods fail on extremely degraded sites destroyed by shrimp farming, mining and over-harvesting (Elster, 2000). Gedan and Silliman (2009) call for a paradigm change away from terrestrial afforestation techniques towards restoration that is adapted to mangrove dynamics. Minimizing competition among mangrove seedlings during the restoration of extremely degraded site might not be necessary because environmental stress factors influence tree growth more than competition for limited resources. On the contrary, facilitative tree interaction might be important for successful restoration because trees can ameliorate environmental stress (Fajardo and McIntire, 2011).

Although mangroves are able to reproduce already in a very young age (Clarke, 1995), the natural regeneration of mangrove forests may occur very slowly under arid and hypersaline conditions (McKee et al., 2007). The application of nurse plants in the restoration of degraded mangrove forests has the potential to solve the problem of severe mortality among planted seedlings (Gedan and Silliman, 2009). Besides the use of nurse plants, the use of facilitative intraspecific interactions could also open up new possibilities for the development of cluster planting arrangement in contrast to even-spaced planting techniques which seek to lower competition.

1.1 RESEARCH OBJECTIVES

The general objective of this dissertation was to improve mangrove restoration by understanding regeneration processes and local plant-plant interaction of *Avicennia germinans* under harsh environmental conditions. I conducted this study in a recently degraded mangrove site which is regenerating following a stand-replacing disturbance. Point pattern analysis and point process modeling were used to infer regeneration and interaction processes from mapped forest structures (Figure 1.1). Consequently, the overall research question of this dissertation can be formulated as following:

How does the interaction among *A. germinans* seedlings and trees influence forest development?

In the first study (chapter 2), I investigated two phases in the life cycle of *A. germinans*, seedling establishment and tree recruitment during the recolonization of a degraded site. The objective was to analyze the relative influence of multiple biotic factors on the density of *A. germinans* seedlings and recruited trees. Due to their tidal dispersal, mangrove propagules depend on entrapping structures, such as salt-marsh vegetation cover, to recolonize high-shore areas (McKee et al., 2007; Milbrandt and Tinsley, 2006). I compared the influence of crown cover and stem position of conspecific *A. germinans* trees, as well as the influence of herbaceous salt-marsh vegetation and coarse wood debris on seedling establishment and tree recruitment based on following research question:

How do *A. germinans* trees compared to herbaceous salt-marsh vegetation and coarse wood debris influence the density of *A. germinans* seedlings and recruits?

The stress gradient hypothesis states that plant interaction is more likely to have a positive effect on plant growth and survival under harsh conditions (Callaway and Walker, 1997). In the second study (chapter 3), I analyzed how intraspecific interaction among *A. germinans* trees is associated with tree growth in order to find out whether trees compete or facilitate one another under the influence of high salinity, low water availability and high solar radiation based on following research question:

How does the interaction among *A. germinans* trees influence their size, growth and crown displacement under harsh environmental conditions?

In the case of monospecific plant communities, aggregated plant distributions can be the product of short-range dispersal and facilitative interactions, or both processes (Velázquez et al., 2014). In the third study (chapter 4), I used point process modeling to infer about dispersal processes and the influence of *A. germinans* trees on seedling establishment and tree growth in more detail. The objective was to distinguish the influence of propagule dispersal and tree-seedling interaction on the spatial distribution of *A. germinans* seedlings and trees in a high-elevated area which is rarely inundated. Accordingly, I formulated the following two research questions:

How are propagules of *A. germinans* dispersed by tidal inundations in a rarely inundated area?

How is the establishment of *A. germinans* seedlings influenced by conspecific trees after dispersal?

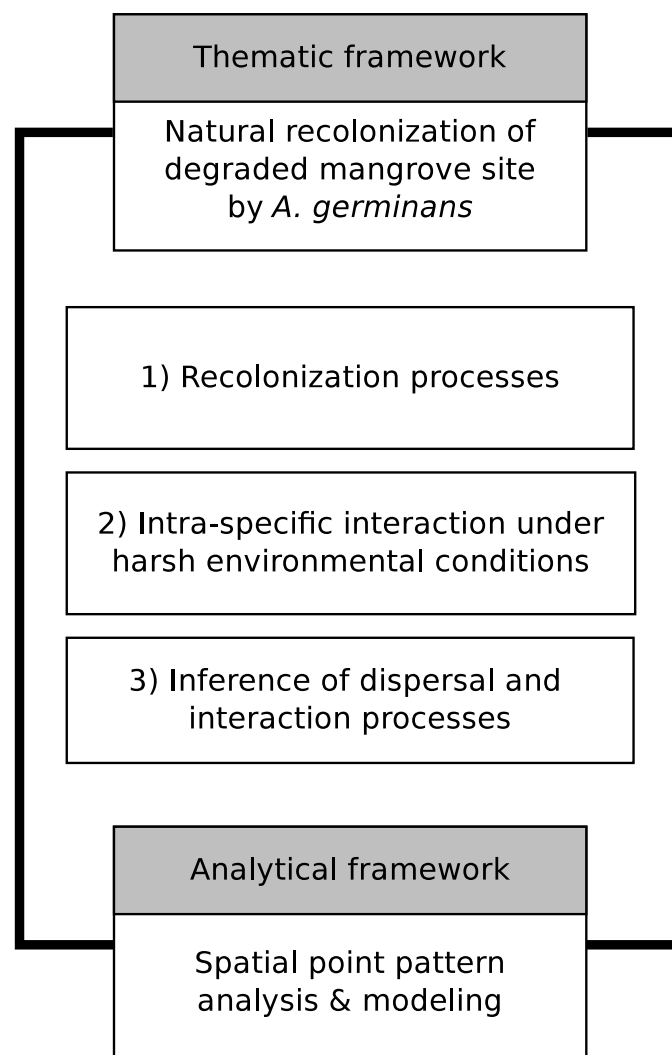


Figure 1.1: Thesis structure.

1.2 *AVICENNIA GERMINANS* - A MANGROVE PIONEER SPECIES

The physiology of mangrove trees is well-adapted to their coastal environment. Aerial roots and salt excretion enable trees to cope with frequent tidal flooding and salinity (Tomlinson, 1994). In addition to be able to survive under extreme tidal conditions, mangroves do also disperse over large distance due to two distinct reproductive mechanisms, vivipary and hydrochory (ibid.). Most mangrove propagules are buoyant and mainly dispersed by water, i.e. hydrochorous, which enables them to disperse over large distances by tidal and coastal currents (ibid.). The propagules of most mangrove species are viviparous which means that they germinate while still attached to their parent tree (Saenger, 2002, p. 85).

The black mangrove, *Avicennia germinans* (L.) L. is at the center of this dissertation due to its ability to thrive under the most extreme environmental conditions compared to other mangrove species of the Neotropics (Sobrado, 1999). *A. germinans* is distributed along the Atlantic coasts of tropical America, the Pacific coast from Mexico to Peru and the coasts of western Africa (Saenger, 2002, p. 15). As a member of a widespread family of mangrove pioneers, *A. germinans* is able to colonize bare tidal flats rapidly (Proisy et al., 2009).

Although *A. germinans* is able to resprout from stumps through coppicing, it depends on propagules for colonization and forest regeneration (Saenger, 2002, p. 120). *A. germinans* propagules are semi- or crypto-viviparous, i.e. embryos germinate while still attached to their parent tree but remain enclosed in the pericarp (ibid., p. 85). *A. germinans* propagules are a fleshy capsule containing an individual seed (ibid.). A fresh propagule weights approximately 1.0 g (fresh weight) and is on average 19 mm long (Sousa et al., 2003). Depending on the tidal regime propagules either establish within the seed shadow or are dispersed hydrochorously after the abscission from their parent tree.

In contrast to most other mangrove species, *A. germinans* is able to tolerate both very high soil pore-water salinity of 100 ‰ and drought (Sobrado, 1999), and has its niche in higher elevated and less frequently inundated sites (Menezes et al., 2008). *A. germinans* stands in elevated terrain are flooded infrequently and are consequently prone to salt accumulation during extreme drought periods because of high evaporation rates and the lack of freshwater (McKee, 1995b). Hypersalinity and limited water availability lead to decline in photosynthetic activity, reduced height growth and more efficient water use (Lovelock and Feller, 2003). *A. germinans* trees experience several physiological changes under hypersaline conditions such as a decline in the rate of photosyn-

thesis and growth as well as an increase in water use efficiency (Krauss et al., 2008). Its high morphological plasticity enables *A. germinans* to cope with these physiological constraints and adapt to different environmental conditions. Under harsh environmental conditions *A. germinans* trees are stunted and shrub-like, whereas under benign conditions they grow tall and form a clear bole (Figure 1.2, Suarez and Medina, 2005). These dwarf mangrove forests reach heights of less than 2.5 m (Menezes et al., 2008) and are usually comprised only of *A. germinans*, although individual *Laguncularia racemosa* trees can be found (Love-lock and Feller, 2003). Furthermore, halophytic plants are associated with these dwarf forests because closed forest canopy is limited to small areas. Two exemplary succulent herb species are *Blutaparon portulacoides* (Figure 1.3a) and *Sesuvium portulacastrum* (Figure 1.3b).

1.3 SPATIAL POINT PATTERN ANALYSIS

Spatial point pattern analysis and modeling are increasingly applied to answer a variety of questions in forest ecology, such as regeneration and stand dynamics (Fajardo et al., 2006; Stoyan and Penttinen, 2000; Wiegand et al., 2009), competitive and facilitative tree interaction (Fajardo and McIntire, 2011; Getzin and Wiegand, 2007; Getzin et al., 2006; Getzin et al., 2011), as well as species composition and biodiversity (Perry et al., 2008; Perry et al., 2013). The spatial distribution of tree stems and their attributes are the results of numerous ecological processes, such as seed dispersal, intraspecific and interspecific competition and facilitation, and environmental heterogeneity (Barot et al., 1999). Horizontal forest structures can be simplified to a discrete set of points on a two-dimensional space which represent the location of tree stems or crown centers (Figure 1.4a). Spatial point pattern analysis enables us to analyze the observed point pattern and to infer underlying ecological processes from their spatial distribution (Law et al., 2009; McIntire and Fajardo, 2009; Perry and Enright, 2006).



(a)



(b)

Figure 1.2: *A. germinans* dwarf forest (a) and shrub-like *A. germinans* tree (b) in the study site.

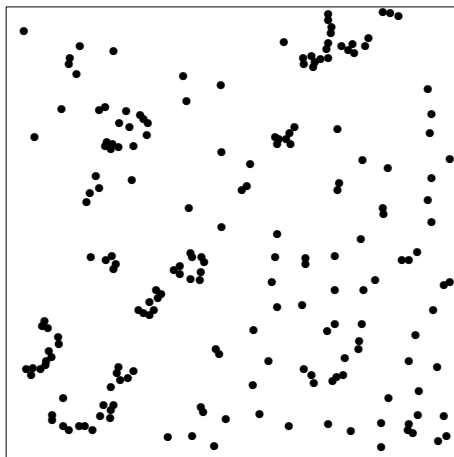


(a)

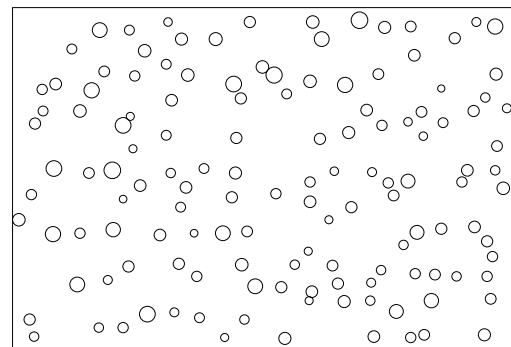


(b)

Figure 1.3: The succulent salt-marsh herb species (a) *Blutaparon portulacoides* (Stefani, 2006) and (b) *Sesuvium portulacastrum* (Anonymous, 2013) associated with mangrove forest.



(a)



(b)

Figure 1.4: Examples of unmarked and marked point patterns of forest stands: (a) seedlings and saplings of California redwood trees (Strauss, 1975) and (b) Norwegian spruce trees with diameter at breast height as mark in Tharandt forest (Stoyan et al., 1987).

Attributes of point patterns are not limited to describe the location of points but can further characterize qualities of points as well as external spatial co-variates (Illian et al., 2008, p. 4). Additional attributes which are attached to points are referred to as 'marks'. Marked point pattern can provide more detailed information than unmarked point patterns which only contain information about point locations. Marks can contain either qualitative (categorical) data, such as tree species or size classes (e.g. seedling, sapling or tree), or quantitative (continuous) data, such as tree size (e.g. diameter or height) or tree growth

(Figure 1.4b). Information about the spatial distribution of point patterns can indicate mortality processes in order to understand self-thinning processes (Kenkel, 1988) or recruitment processes following short-range seed dispersal (Wiegand et al., 2007). Whereas unmarked point patterns can only describe tree regeneration and mortality processes, marked point pattern can be used to analyze spatial effects on tree size, growth, life stage and other traits. Spatial point pattern analysis also provides tools to test the dependency of point distributions on spatial covariates, such as topography, soil conditions or rainfall.

Summary statistics are most frequently used tools to quantify the spatial properties of point patterns. On the one hand, numerical summary statistics, e.g. Clark-Evans index, are used to describe the arrangement of a point pattern with a single-valued index (Illian et al., 2008, p. 40). On the other hand, the recently developed functional summary statistics describe point patterns as a function of spatial scale, e.g. how strong and at what scales trees are clustered, regularly or randomly distributed. Functional summary statistics, such as Ripley's K -function $K(r)$ or the pair-correlation function $g(r)$, can provide more information about the existence of spatial structure at certain scales (ibid., p. 40). Due to this advantage I used in this thesis only functional summary statistics. Multiple summary statistics should be employed because spatial patterns are the result of a complex set of processes (Wiegand and Moloney, 2013, p. 8).

In contrast to descriptive summary statistics, point process models can be used to test assumptions and hypotheses regarding the spatial distribution of observed point patterns (Wiegand et al., 2007; Wiegand et al., 2009). Point processes are stochastic models which generate particular point patterns consisting of a finite set of points within a bounded window (Diggle, 2013). Underlying ecological processes can be investigated by fitting a mathematical point process to the observed point pattern of trees. A regular distribution of trees is commonly understood as the result of competition, clustered tree distribution can be caused by facilitation, local seed dispersal or environmental heterogeneity, and random distributions are used as null hypothesis because they indicate the absence of ecological processes. These ecological processes can be simulated with the corresponding point process (Figure 1.5).

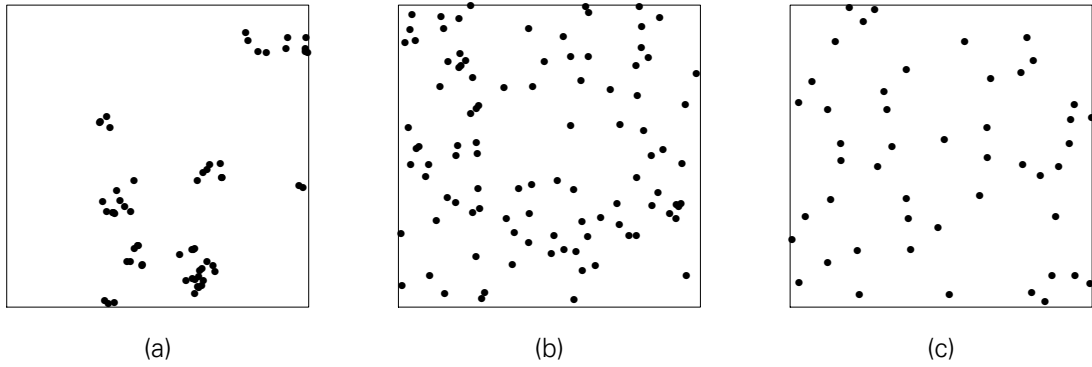


Figure 1.5: Examples of point process realizations: (a) clustered process, (b) random process and (c) regular process.

1.4 STUDY SITE

The study was conducted in the central area of the Ajuruteua peninsula, State of Pará, Northern Brazil (Figure 1.6). The peninsula is located between the estuaries of the Taperaçu and Caeté River to the north of the city of Bragança. The peninsula is part of a continuous mangrove area along the South American coast and dominated by *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia germinans* (Menezes et al., 2008). The coastal ecosystem of Bragança is influenced by a distinct dry season with a monthly precipitation below 60 mm which lasts from August until December, and a rainy season above 350 mm which between January and July (Souza-Filho et al., 2009). Average annual temperature lies between 25.2-27.4°C (Krause et al., 2001).

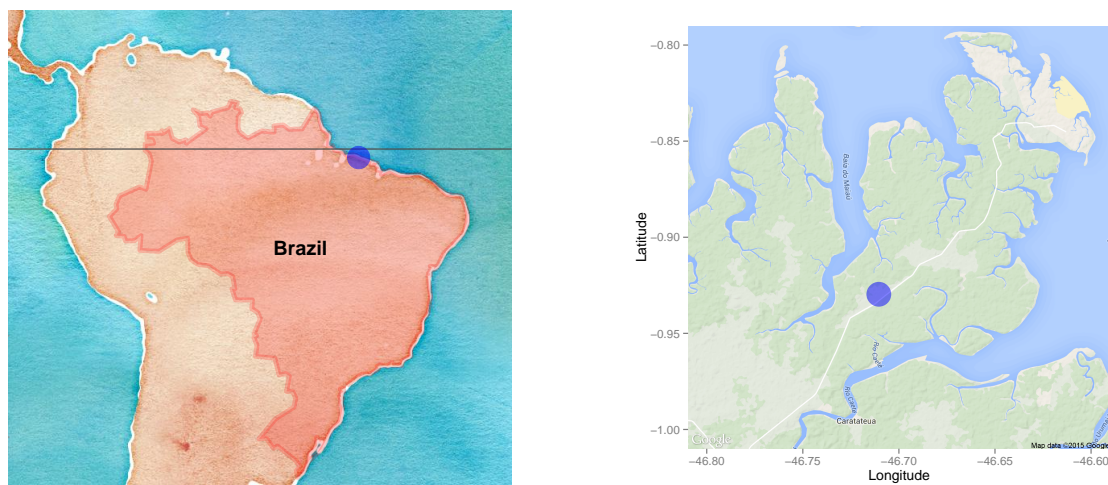


Figure 1.6: The study area is located on a degraded mangrove area in the Bragança peninsula, State of Pará, Brazil.

The study site is located in a higher elevated and rarely inundated area, which was covered by undisturbed mangrove forest until the construction of a 25 km long highway section in 1974 (Cohen and Lara, 2003). The paved road was constructed in the center of the peninsula in order to facilitate transportation between the coastal village Ajuruteua and Bragança. The road disturbed the water regime by interrupting the tidal flow from the Caeté river, which caused a rapid die-back of the mangrove forest on the western side of the road. Consequently, large areas of the mangrove vegetation died and the degraded area consisted of dry mudflats, which are associated with high pore-water salinity (Krause et al., 2001). Following the stand-replacing disturbance, no management activities, such as the restoration of the former hydrological regime and planting of mangrove seedlings, were undertaken to rehabilitate the degraded mangrove forest. Thus, the study site is in a process of natural recolonization. Figure 1.7 and 1.8 illustrate the structural development of the *A. germinans* dwarf forest in the study site.

After the degradation of the *A. germinans*-dominated forest (Mehlig et al., 2010), the resulting bare area was recolonized gradually by a dwarf mangrove forest consisting mostly of shrub-like *A. germinans* and scattered *L. racemosa* of heights below 2 m (Cohen and Lara, 2003). In comparison, undisturbed *A. germinans* stands on the same peninsula can reach DBH 100 cm and a tree height of more than 30 m (Menezes et al., 2008). Propagules were dispersed while the area was inundated by infrequent spring tides from the river Taperaçu on the western side. Due to hypersalinity (> 100 ‰ at 50 cm sediment depth) and high ground temperatures (> 40°C), the height growth of monospecific *A. germinans* forests is limited to 2-5 m (Menezes et al., 2008; Vogt et al., 2014). The extreme conditions prevented the establishment of other mangrove tree species (Medina and Francisco, 1997). Patches of succulent salt-marsh vegetation, specifically *B. portulacoides* and *S. portulacastrum*, are scattered throughout the dwarf forest because shrub-like trees are sparse and the canopy cover is low (Menezes et al., 2008). I did not observe any form of herbivory during my fieldwork.

1.5 DATA COLLECTION

In 2011, six 20 x 20 m² plots (1A, 1B, 2A, 2B, 3A and 3B) were established near the highway between Bragança and Ajuruteua (Figure 1.9 on page 16). The plots were at least 20 m apart from one another. Plots were located along a gradient

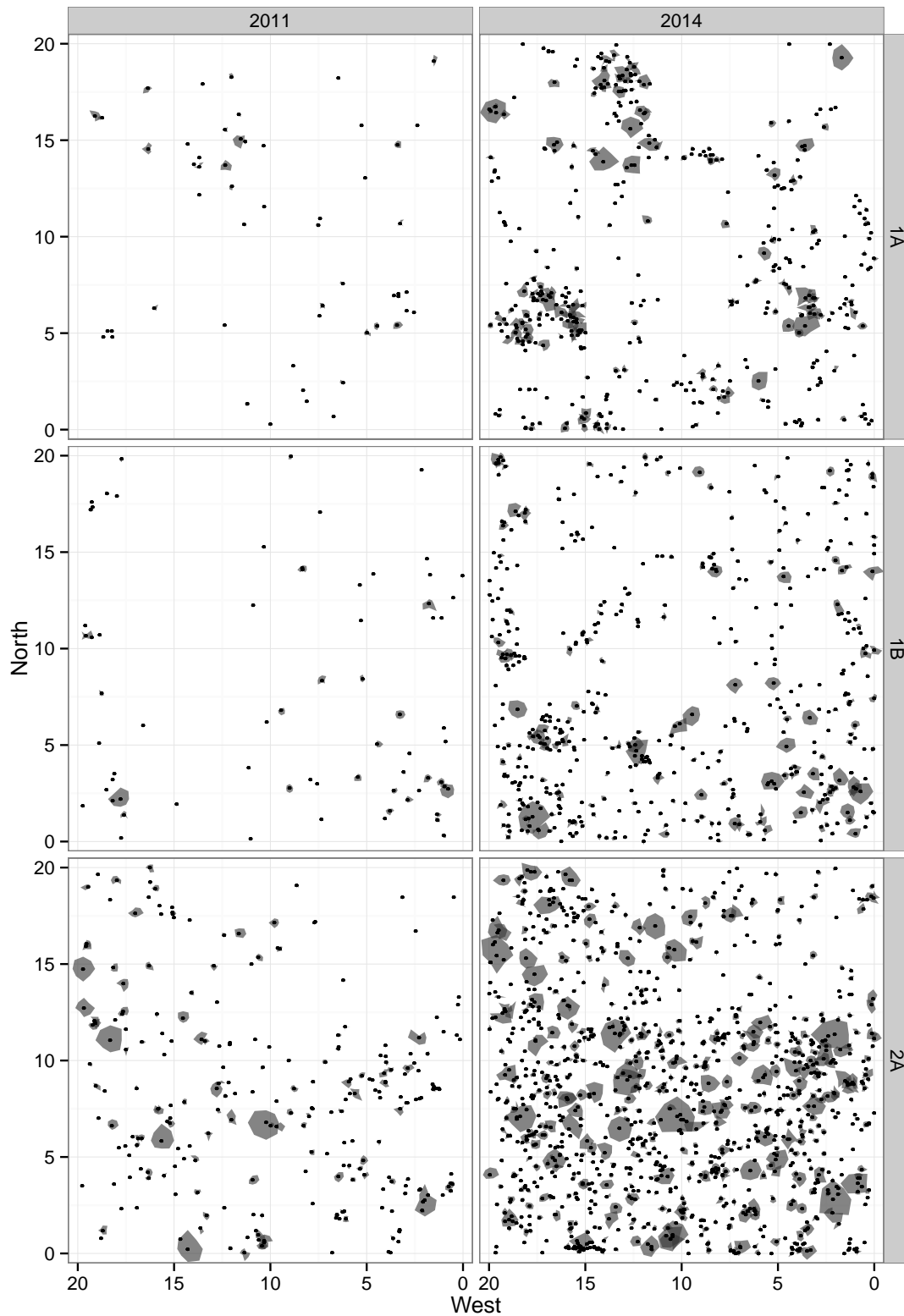


Figure 1.7: Crown projection map the forest plots 1A, 1B and 2A in 2011 and 2014 (plot size: 20 x 20 m²). Grey areas represent the horizontal tree crown area. Black dots represent tree stem coordinates of each tree at the ground level. All trees were shrub-like and multiple-stemmed.



(a)



(b)



(c)



(d)



(e)



(f)

Figure 1.8: Ground view of the forest plots 1A (top), 1B (middle) and 2A (bottom) in 2011 (left) and 2014 (right) from coordinate 0,0 towards NW.

of tree density to represent the forest conditions influencing regeneration processes occurring within the area. The plot locations were selected based on a satellite image analysis of IKONOS images with a resolution of 1 m x 1 m (Vogt et al., 2014). The plots 1A, 1B and 2A in the lesser developed forest area were remeasured in 2014. Both data collections were carried out between February and April in the rainy season.

The stem position of all mangrove plants was mapped on a Cartesian coordinate system using 2 measurement tapes at 2 m distance and a yardstick. Coordinates were measured on a 1 cm x 1 cm grid. The minimum distance between plants was 1 cm. This mapping method was reliable, inexpensive and accurate but very time-intensive. Plants with less than three branches were classified as seedlings, whereas plants with at least three branches were classified as trees. Only seedlings without cotyledons were measured, which means that these seedlings were already several months old (Rabinowitz, 1978a). Furthermore, all trees first recorded in 2014 were classified as recruited trees, whereas tree which were mapped already in 2011 were classified as non-recruited trees. The basal stem diameter at ground level, height, and maximum crown extent of all trees were measured. All trees in the study area were shrub-like shaped and multi-stemmed with a clear length of not more than approximately 3 cm. In addition, only a few trees reached a height of 1.3 m, which is the common height for diameter measurements (DBH - diameter at breast height). I decided to measure the basal stem diameter at ground level because trees did not reach this height. Thus, this measurement enabled me to compare the size of differently-shaped trees across the study area. Only in 2014, the length of ten last internodes along the main branch were recorded by measuring the distance between main bud scars along the branch. In 2011, herb coverage and wood debris were visually mapped in a grid of 10 cm². An overview of the measurements is provided in Table 1.1. For each of the following three studies different parts of this data set were utilized (Table 1.2).

Table 1.1: Overview of field measurements.

Year	Position	Basal stem diameter	Height	Crown extent	Internode length	Herb vegetation cover	Wood debris	Plots
2011	✓	✓	✓	✓		✓	✓	1A,1B, 2A, 2B, 3A, 3B
2014	✓	✓	✓	✓	✓			1A,1B, 2A

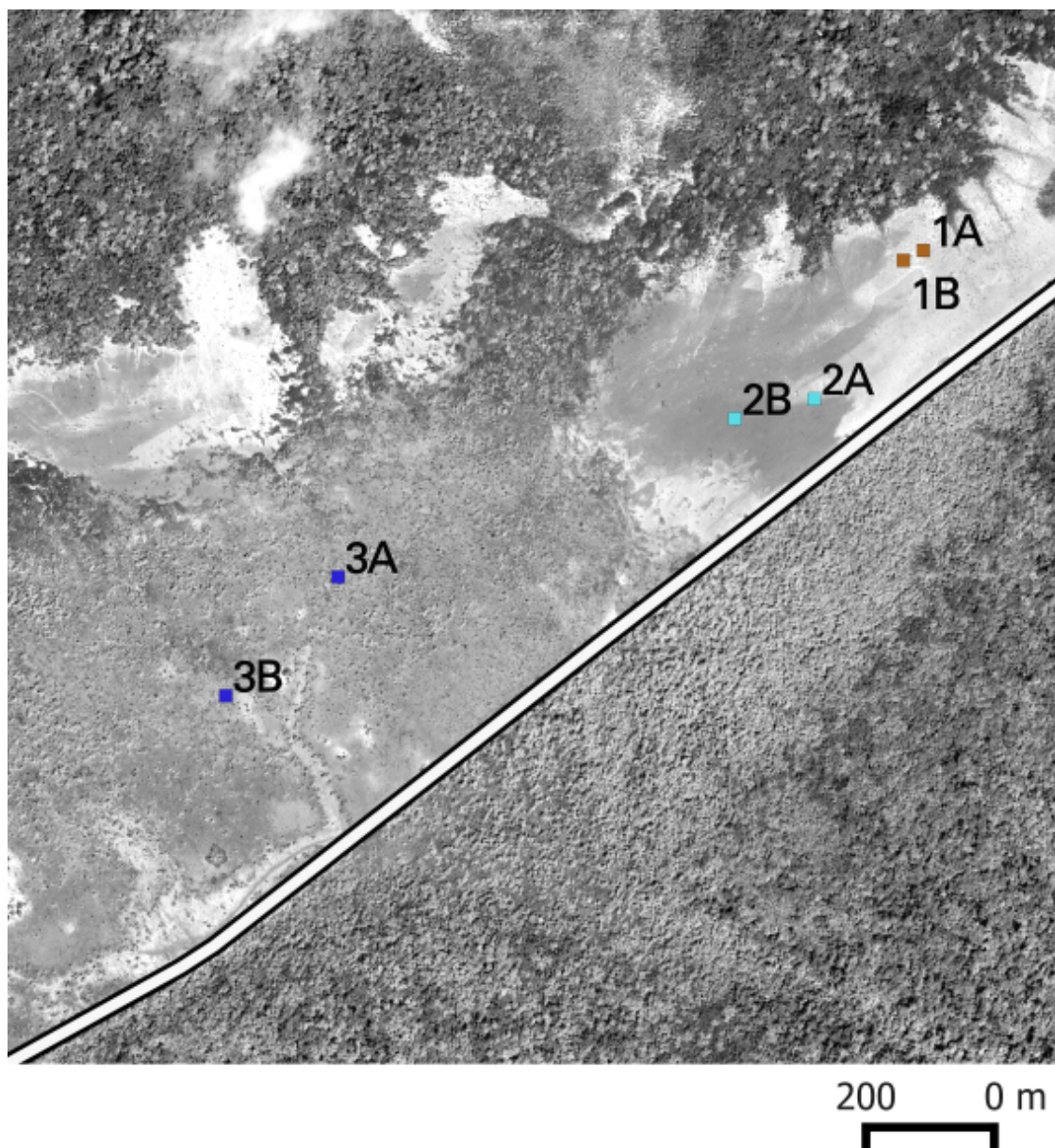


Figure 1.9: Location of all plots along a gradient of tree density in degraded mangrove area on the north-western site of the road (IKONOS 1 m x 1 m resolution, 2007).

Table 1.2: Data usage in each chapter.

Chapter	2011						2014		
	1A	1B	2A	2B	3A	3B	1A	1B	2A
2	✓	✓	✓	✓	✓	✓	✓	✓	✓
3							✓	✓	✓
4			✓	✓	✓	✓	✓	✓	✓

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2 DRIVING PROCESSES OF *AVICENNIA GERMINANS* ESTABLISHMENT AND RECRUITMENT PATTERNS DURING RECOLONIZATION

ABSTRACT

Recolonization of degraded sites is the first phase in mangrove forest regeneration following a stand-replacing event. Processes which take place in this first stage have great influence on the following forest development. The positive effect of herbaceous vegetation and canopy cover on mangrove regeneration of degraded sites is well-known. However, the effect of these factors on mangrove seedling establishment were studied isolated and there effect on tree recruitment is unknown. The objective of this study was to analyze the spatial dependency of *A. germinans* seedling establishment and tree recruitment on local biotic factors during forest regeneration.

Gibbs point process models were used to analyze the dependency of point pattern on spatial covariates, such as herbaceous vegetation cover and tree canopy cover, and to investigate interaction among tree recruits. The validity and sensitivity of each model was assessed using residual, leverage and influence diagnostic tools as well as Q-Q plots and simulation envelopes.

Most seedlings established adjacent to trees, especially under and adjacent to their crown cover. Moreover, seedling density was higher within patches of the herbaceous salt-marsh plants *Blutaparon portulacoides* and *Sesuvium portu-*

lacastrum than in uncovered areas. The ground vegetation did not negatively influence the subsequent development of *A. germinans* which resulted in a higher density of recruited trees in herb patches. In addition, tree recruitment occurred in clusters.

In degraded mangrove areas, herbaceous salt-marsh vegetation trap propagules and facilitate trees by ameliorating harsh environmental conditions. Spatial aggregation of recruited trees and the clustering of seedlings under tree crowns suggests that interactions were not competitive and possibly facilitative. Herbaceous vegetation cover should be utilized during the restoration of degraded mangroves to assist rapid natural regeneration.

2.1 INTRODUCTION

Forest regeneration is the sequence of dispersal, emergence, establishment and survival which link the stages in the life-cycle of trees, including seeds, seedlings, saplings and adults (Clark et al., 1999b; Wang and Smith, 2002). Numerous studies have investigated the regeneration dynamics of mangroves by analyzing the establishment, subsequent survival of a seedling population and the recruitment of juvenile trees into the adult population (Balke et al., 2011; Blanchard and Prado, 1995; Clarke and Allaway, 1993; Krauss et al., 2007; Roth, 1992). Multiple factors influence the regeneration dynamics of mangrove forests from seed disposition until recruitment into the adult population, such as the existence of well-developed stands which determine the amount of supplied propagules, flooding and inundation regimes which control propagule dispersal (Clarke and Allaway, 1993; Clarke et al., 2001; Ellison and Farnsworth, 1993; Rabinowitz, 1978b; Rabinowitz, 1978c), crabs which predate on propagules (Lindquist and Carroll, 2004; McGuinness, 1996; McKee, 1995a; Osborne and Iii, 1990), herbaceous vegetation which entrap seedlings establishment (McKee et al., 2007; Milbrandt and Tinsley, 2006; Peterson and Bell, 2012) and the impact of environmental conditions, such as salinity and temperature, on the early survival and development of established seedlings (Ball, 2002; Krauss et al., 2007; Krauss et al., 2008; McKee, 1995a; Sherman et al., 2000; Sobrado, 1999). However, these numerous influences of local neighborhood and environmental conditions have been studied isolated although they occur often simultaneously and interactively.

Two processes shaping early forest development, seedling establishment and tree recruitment (Clark et al., 1999b), are conceptualized in Figure 2.1. Mangrove propagules either establish nearby their parent tree or are dispersed hy-

drochorously through tidal transportation and establish only after settlement. The hydrochorous dispersal of mangrove propagules is driven by the propagule's shape and its hydrodynamical properties (De Ryck et al., 2012), as well as the influence of dispersal vectors, such as tidal flow, freshwater discharge and wind (Di Nitto et al., 2013). The location of seedling establishment is first determined by factors influencing settlement of propagules. In mangrove forests, the settlement of floating propagules is influenced by trapping structures (Di Nitto et al., 2013; McKee et al., 2007), whereas the survival of seedlings is influenced by the microhabitat within which the seed settles and in which it further develops (Clark et al., 2013). Locations with appropriate environmental conditions for the establishment of seedlings are also referred to as safe sites (*sensu* Harper, 1977). Herbivory by insects and decapods can influence propagule and seedling survival before and after propagule dispersal (Elster et al., 1999; Ozaki et al., 1999). Forest conditions, such as the spatial distribution of larger trees and abiotic site conditions, influence the pattern of seedling establishment by concentrating regeneration in certain forest areas (Haase et al., 1996; Mast and Veblen, 1999; Szwagrzyk et al., 2001; Zackrisson et al., 1995). The survival and recruitment of trees are determined by the availability of sunlight, nutrients (Elison and Farnsworth, 1993; Smith III, 1987) and sensitivity to environmental stress factors (Koch and Snedaker, 1997; Krauss et al., 2008; McKee, 1995a; McKee, 1996; Youssef and Saenger, 1998).

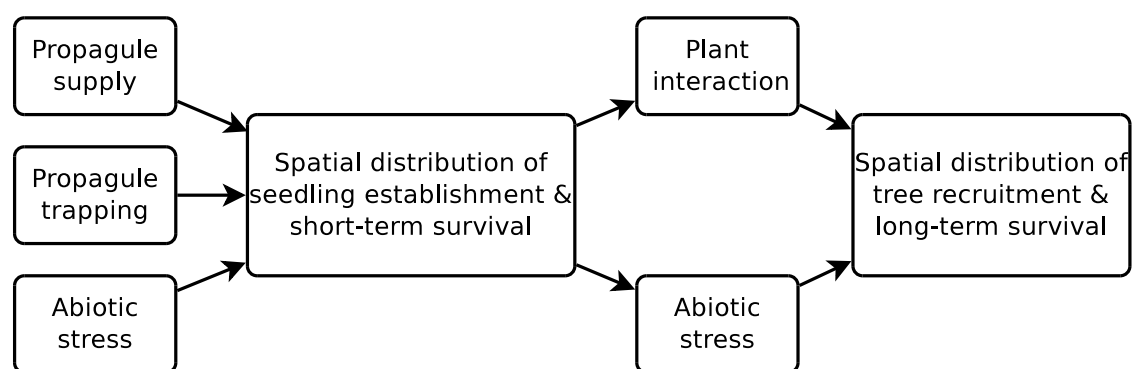


Figure 2.1: Conceptual framework for spatial point modeling.

Spatial distribution of plants are expected to emerge from interacting ecological processes such as dispersal, regeneration, competition or facilitation. Spatial point pattern analysis can be used to extract information from observed spatial pattern and to infer underlying processes from plant distributions. Point process models provide the ability to test the dependence of observed plant distributions on spatial covariates, for example soil conditions, canopy cover or elevation. Therefore, these models can be used to analyze the influence of seedling and recruited trees on biotic and abiotic factors (McIntire and Fajardo, 2009;

Wiegand and Moloney, 2004; Wiegand et al., 2007).

The processes influencing the settlement of propagules following their dispersal also influence recruitment and the spatial structure, species composition and dynamics of the forest community (Clark et al., 1999b; Fajardo et al., 2006; Harper, 1977). This fact makes it easier to determine underlying ecological processes by analyzing the observed spatial pattern of mangrove seedlings and trees. Ecological processes acting on mangrove trees have an immediate impact on the community's spatial pattern and are detectable with spatial statistics.

The regeneration ecology of *Avicennia* is special in three aspects. First, trees depend on generative reproduction and have no ability to reproduce vegetatively (Tomlinson, 1994). Second, propagules are semi-viviparous, i.e. germinate while attached to the parent tree, and exhibit no period of embryo dormancy (Clarke and Allaway, 1993; Tomlinson, 1994). Third, the dispersed propagules are not buried as seed banks but establish rapidly soon after settling (Balke et al., 2011). Therefore, the spatial pattern of observed seedlings constitutes the entire seed stock and the development of the propagule is entirely determined by the surrounding environment in which it settles.

Abiotic conditions, especially salinity, have a great influence on seedling establishment and survival. Correspondingly the height of mangrove trees is highly responsive to porewater salinity and hence an indicator of environmental stress factors (Méndez-Alonzo et al., 2008; Sobrado, 1999). Trees growing under more saline conditions require more energy for water uptake. This limited water availability results in stunted growth and lower tree heights (Peters et al., 2014; Vovides et al., 2014).

Although mangrove propagules can be dispersed over long distance, they often strand and establish nearby parental trees (McGuinness, 1996; Rabinowitz, 1978a). Intraspecific interference with existing vegetation can have negative and positive outcomes for the upcoming regeneration. Mortality is usually highest in the seedling phase because seedlings are more vulnerable to predation and environmental stress (Clark et al., 1999b; Clarke, 1993). Protective microhabitats can improve the survival rate and growth of seedlings in stressed environments (Maestre et al., 2001; Pugnaire et al., 1996). For instance, canopy cover can ameliorate the impact of extreme environmental stress on seedlings either through direct shading, which lowers plant transpiration and tissue damage caused by solar radiation, or through indirect shading, which increases soil moisture (Fajardo and McIntire, 2011). Like most mangrove species, *Avicennia germinans* is light-demanding and requires sunlight in order to develop following the seedling phase (Ball, 1988). This would suggest that recruited trees are competing for

sunlight with their immediate neighbors. However, under hypersaline conditions water uptake and photosynthetic rates of *A. germinans* are limited and hence the response to incident sunlight.

Although mangrove communities are species-poor, herbaceous vegetation, such as salt-marsh plants, can be found along forest edges and gaps where sunlight reaches the forest floor (Tomlinson, 1994). After stand-replacing events and large-scale forest die-backs, herbs can invade mudflat areas rapidly after the upperstorey canopy disappeared (Milbrandt and Tinsley, 2006). Herbaceous halophytes, such as *Batis maritima*, are able to recolonize extensively degraded forests (McKee et al., 2007). It has been shown that the presence of these initial colonizers improve the trapping and retention of dispersing propagules as well as the promotion of seedling survival and growth through amelioration of soil conditions (Peterson and Bell, 2012). Mangrove propagules are dispersed hydrochorous, i.e. by tidal waves. Thus, propagule retention is an important prerequisite for seedling establishment because mangrove propagules have to strand in order to root and establish. Without entrapping vegetation on the ground propagules remain buoyant, are drawn back with the next tide and not able to root (Rabinowitz, 1978a). *Avicennia* propagules can float for long periods in salt water and have a longevity of 110 days (Dodd et al., 2000). Hence, the existence of herbaceous halophytes can accelerate the natural recovery of disturbed mangrove forests (Day and Wright, 1989; McKee et al., 2007; Milbrandt and Tinsley, 2006). Consecutive studies have shown that the habitus and structure of herbaceous salt-marsh vegetation determine their capacity to entrap certain mangrove propagules (Peterson and Bell, 2012). For example, the propagules of *Rhizophora mangle* weight approximately 17.5 g (fresh weight) and are on average 223 mm long, whereas propagules of *A. germinans* weight approximately 1.0 g (fresh weight) and are only 19 mm long (Sousa et al., 2003).

Remaining logs of the pre-disturbance forest stand are scattered across the site. This coarse wood debris may trap propagules and facilitate seedling establishment similar to the herbaceous vegetation. In addition, the decaying organic material may enrich the surrounding soil and improve the microhabitat.

Besides the availability of suitable habitats for seedling establishment, forest regeneration is also determined by supply of propagules to the forest stand. Under harsh environmental conditions, *A. germinans* fruits already in a very young age (Clarke, 1995) which has been observed in the study site as well.

In addition to external environmental factors, trees also interact with neighboring trees. Distinct patterns of tree distribution are one outcome of tree interaction and, thus, can be identified with spatial pattern analysis after accounting for external environmental factors (McIntire and Fajardo, 2009; Wiegand et al.,

2007). A random distribution of trees would suggest that trees do not interact strongly. Regular tree distribution is seen as a result of intense competition among trees for limited resources (Fortin and Dale, 2005). On the other hand, aggregated or clustered tree patterns indicate either facilitative tree interaction or short-distance distribution of propagules (Lin et al., 2012; Tirado and Pugnaire, 2003). Following the stress-gradient-hypothesis, which is outlined in more detail in Chapter 3, trees are less likely to compete under harsh environmental conditions and are hence aggregated and not regularly distributed.

The objective of this study is to explore two phases in the life cycle of *A. germinans*, seedling establishment and tree recruitment because of their importance for later forest development. I developed eight hypotheses regarding the influence of biotic factors on the establishment and recruitment of *A. germinans* during the recolonization of degraded sites (independent variables are highlighted bold).

1. **Top height** is positively related to the establishment of seedlings and recruitment of trees.
2. Establishment of seedlings and recruitment of trees is more intense under **tree crown area**.
3. Establishment of seedlings and recruitment of trees is more intense in close proximity to the nearest **tree crown edge**.
4. Establishment of seedlings and recruitment of trees is more intense in close proximity to the nearest **tree stem**.
5. Establishment of seedlings and recruitment of trees is more intense in patches of the succulent **herb species** *Sesuvium portulacastrum* and *Blutaparon portulacoides*.
6. Establishment of seedlings and recruitment of trees is more intense in close proximity to the nearest **wood debris**.
7. **Tree density** is positively related with the establishment of seedlings and recruitment of trees.
8. Recruited trees are aggregated.

I analyzed the dependence of small-scale spatial tree distribution on other biotic factors in early successional mangrove forest stands which are recolonizing a degraded area in Northern Brazil. A better understanding of the mechanisms

which drive forest regeneration is essential for an efficient and effective restoration of degraded mangrove forest ecosystems (McKee, 1995a; McKee et al., 2007).

2.2 DATA ANALYSIS

For a detailed description of data collection procedure see section 1.5 on page 12.

The forest vegetation map of each plot was transformed into a two-dimensional point pattern in which each point represents the stem position of either an *A. germinans* seedling or a shrub-like *A. germinans* tree.

Nine point patterns of three different types, seedlings in a low-density forest stand, seedlings in a high-density forest stand, and recruited trees, were generated in total. The forest maps of 2011 were used to construct six seedling point patterns, which were separated into seedling patterns in forest stands of low (1A, 1B, and 2A) and high (2B, 3A, and 3B) tree density. The forest maps of plots 1A, 1B, and 2A in 2014 were used to construct three point patterns of shrub-like trees which were recruited between the years 2011 and 2014. The plots 2B, 3A, and 3B were not mapped in 2014.

The spatial distribution of seedlings and trees in a forest is the result of various underlying ecological processes, such as habitat association or tree interaction. Point process models were used to test the dependency of three sets of point patterns on biotic variables (see covariates Figure 2.2) in order to infer underlying ecological processes.

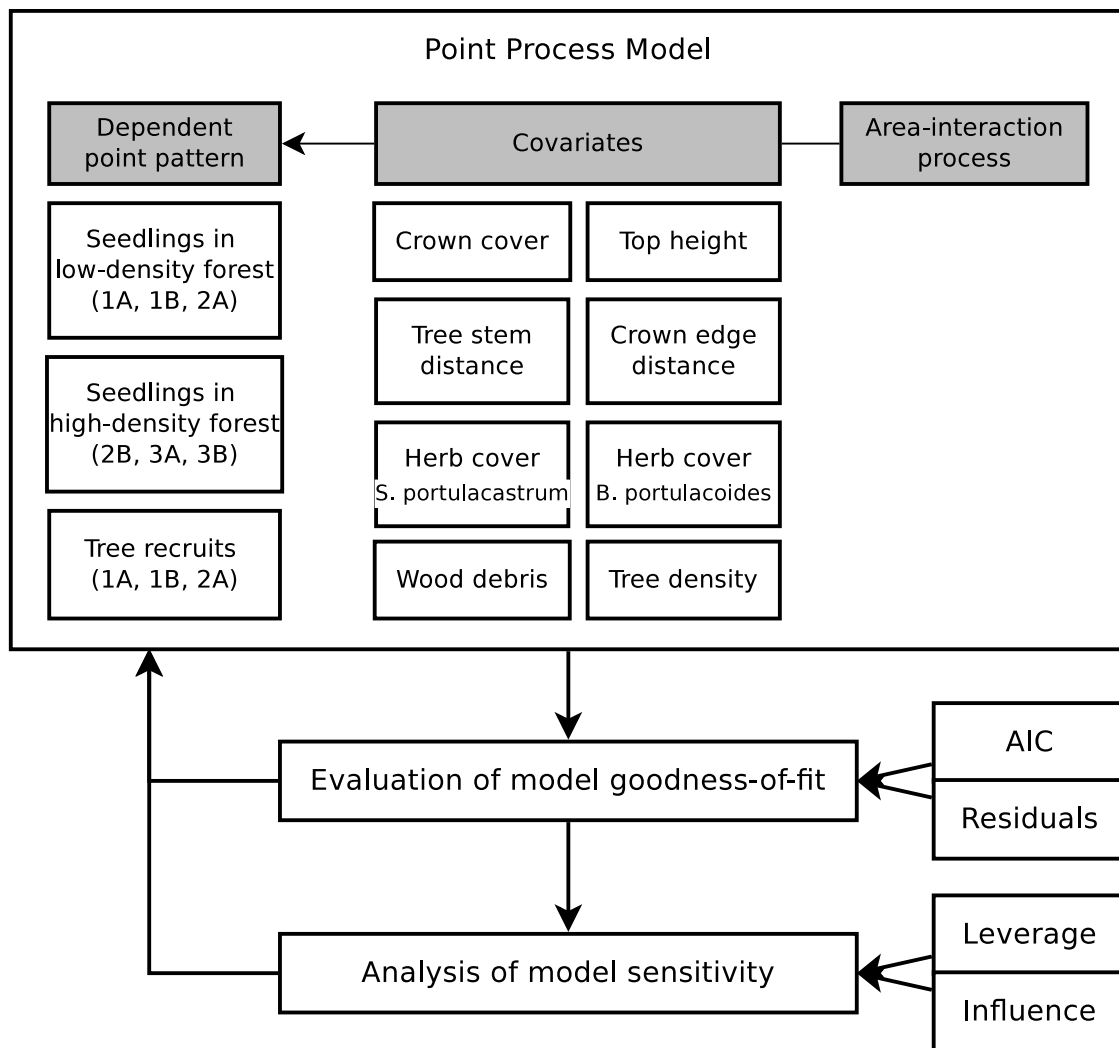


Figure 2.2: Flowchart of point process modeling procedure including model building, evaluation and sensitivity analysis.

2.2.1 GIBBS POINT PROCESS MODELING

Point process model are fitted to generate a point pattern similar to the observed pattern of trees and seedlings in order to identify parameters which result in the best model fit and to test stated hypotheses regarding underlying ecological processes (Wiegand et al., 2007; Wiegand et al., 2009). Furthermore, point process modeling can also be used to simulate and predict point patterns.

Gibbs point processes was the class of point process models which was used to fit the observed spatial distribution of *A. germinans* seedlings and shrub-like recruits. In principle, the fitting procedure of Gibbs model is similar to procedures used for fitting multiple linear models. A great advantage of the Gibbs point process is their wide scope because they allow the integration of spatial trends, dependence on covariates as well as interpoint interactions. Covariates are environmental structures or patterns which may influence the point pattern,

e.g. herbaceous vegetation cover or the distance to the nearest tree.

The intensity λ of a point process describes the mean number of points per unit area. The Gibbs process model fits the conditional intensity $\lambda(u, x)$ which is a function of the location u within the observation window and the point pattern x . Accordingly, $\lambda(u, x)du$ can be understood as the conditional probability that there is a point of the process in the area du at location u given the point pattern outside the area at u (Gelfand et al., 2010, p. 322).

A Gibbs point process with a constant intensity and without interpoint interaction or dependence between points is considered to be a homogeneous Poisson process with conditional intensity

$$\lambda(u, x) = \beta \quad (2.1)$$

where the point pattern x at location u depends on the constant local intensity β (Baddeley et al., 2006, p. 28). Thus, the expected number of points per unit area is constant in each location u and randomly distributed over an area. This assumption of complete spatial randomness and stationarity is unsuitable for many ecological studies. The inhomogeneous Poisson process is used to model the effects of spatial inhomogeneity on the conditional intensity

$$\lambda(u, x) = \beta(u) \quad (2.2)$$

where the local intensity $\beta(u)$ varies in each location u (ibid., p. 28). Therefore, the number of points per unit area depends on location u which corresponds to a spatial trend of point distribution which is for example caused by a gradient of salinity.

Gibbs point processes can also exhibit stochastic interpoint interactions or dependence between points. An area-interaction process has the conditional intensity associated with the presence of two points when the disc area with radius r overlap

$$\lambda(u, x) = \beta \cdot \eta^{-B(u, x)} \quad (2.3)$$

where $-B(u, x)$ is the area of the circular disc of radius r centered on location u which is overlapping with discs of radius r centered at the other points (Figure 2.3; Baddeley and Lieshout, 1995). The area-interaction parameter η can indicate aggregation due to attraction ($\eta > 1$), regularity due to repulsion ($\eta < 1$) or a hard core process with the distance $2r$ ($\eta = 0$). An area-interaction parameter $\eta = 1$ indicates independence between points and is equivalent to a Poisson process (ibid.). I included an area-interaction process (ibid.) in order to model inter-tree interaction among recruited trees due to its similarity to

Fixed-Radius-Neighborhood (FRN) model (Berger et al., 2008).

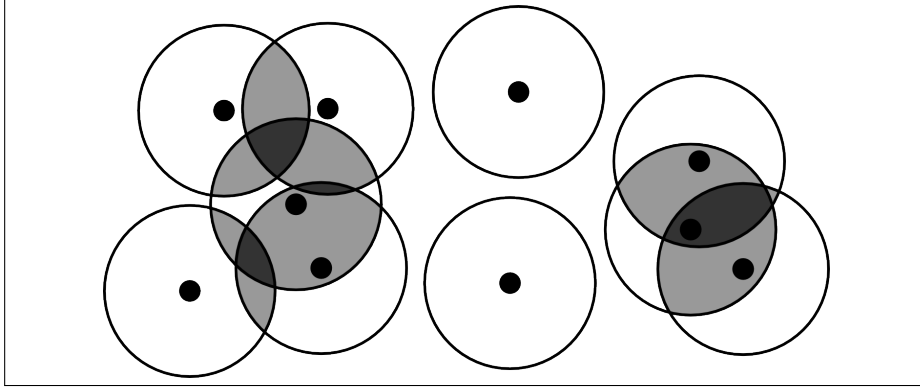


Figure 2.3: Schematic representation of the area-interaction process. Each point is surrounded by a circular disc a fixed radius r . Points interact when their distance is smaller than $2r$. The grey-shaded area represent the overlapping disc areas $-B(u, x)$.

The algorithm to estimate the parameters of each Gibbs point process uses maximum pseudolikelihood because it is easy to compute the conditional intensity $\lambda(u, x)$ (Baddeley and Turner, 2000). It cannot only include interpoint interaction terms, such as Equation 2.3, but can be extended to consider also covariates. The Gibbs point process model fits the conditional intensity of a point pattern as the loglinear function as following

$$\log \lambda(u, x) = \psi S(u) + \varphi V(u, x) \quad (2.4)$$

where $\lambda(u, x)$ is the conditional intensity of a point pattern at the location u , $\theta = (\psi, \varphi)$ are regular parameters to be estimated, $S(u)$ represents spatial inhomogeneity and covariate effects, $V(u, x)$ represents any interpoint interaction process, i.e. the influence of a point at position x on points at location u (Baddeley, 2008, p. 163). The Gibbs model was fitted by incrementally adding a model parameter to the existing model following the Akaike Information Criterion (AIC). Forward stepwise model selection was used because not all possible covariates were available for a backward stepwise selection.

An edge correction was implemented in the model in order to reduce the biased influence of individuals which depend on factors outside the mapped plot area. A margin of 1 m was trimmed in each observed plot which was larger than the estimated area-interaction radius of trees.

COVARIATE EFFECTS

Each point pattern model was comprised of several covariates in order to test the stated hypotheses regarding the conditional density of seedling and recruits

(Table 2.1). In spatial pattern analysis, explanatory variables are generally referred to as spatial covariates regardless of the type of data. Spatial covariates were either categorical maps (Figure 2.4a), such as crown and herb cover, or continuous distance maps (Figure 2.4d), such as distance to the nearest tree, crown edge and wood debris. The pixel maps of herb cover were generated based on field mapping, whereas the map of tree crowns was based on the measured crown extent of each tree (see page 15 for more a detailed description of data collection). The distance map of a point pattern x is a pixel image in which the value of pixel u represents the shortest distance to the nearest point of the point pattern x . Each distance map was based on a different spatial object, including point patterns (Figure 2.4c), pixel images (Figure 2.4a) or line segment patterns (Figure 2.4b). Line segment patterns consist of individual lines which are each described by two endpoints and were used to delineate wood debris distribution. The influence of trees which already existed in 2011, so called non-recruited trees, on seedling establishment and tree recruitment was analyzed by developing three spatial covariates of trees based on the tree stem position, the crown cover and the crown edge. Separate models were constructed for the terms 'distance to nearest tree stem', 'crown cover' and 'distance to nearest crown edge' in order to reduce likely collinearity among these model terms and to analyze which tree attribute influences regeneration most profoundly.

Table 2.1: Covariates for point process modeling of seedling establishment and tree recruitment.

	Description	Data Type (Variable)
Top height	Average height of 10% trees with largest diameter in plot	Numeric covariate (cm)
Tree density	Number of trees in plot	Numeric covariate (number of trees/400 m ²)
Crown cover	Area under tree crown	Pixel image (crown, open)
Herbaceous ground cover	Area covered by herb species <i>S. portulacastrum</i> or <i>B. portulacoides</i>	Pixel image (bare, <i>S. portulacastrum</i> , <i>B. portulacoides</i>)
Crown edge distance	Distance to nearest crown edge from outside crown cover	Distance map (cm)
Tree stem distance	Distance to nearest tree	Distance map (cm)
Wood debris	Distance to nearest wooden debris	Distance map (cm)

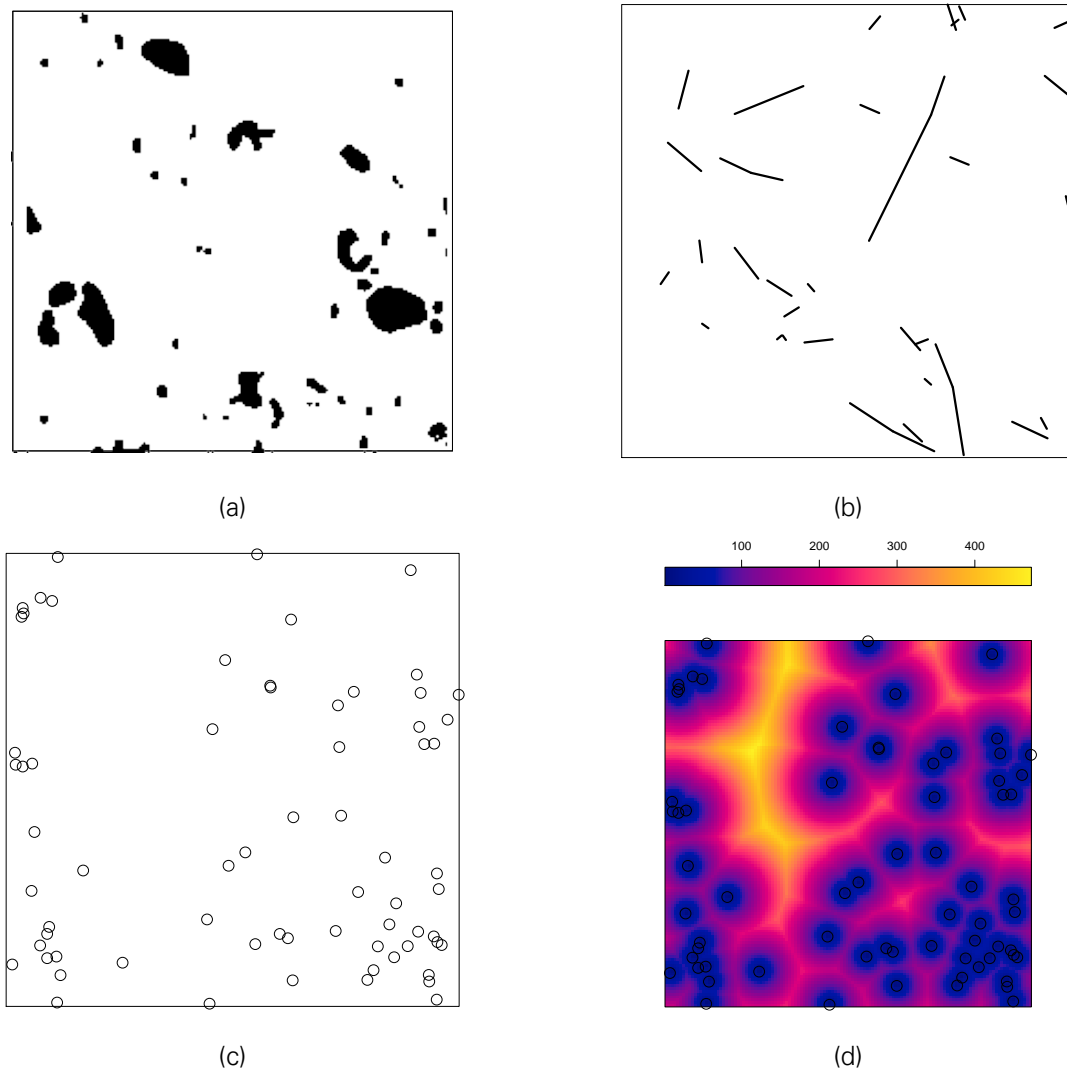


Figure 2.4: Example of a pixel image (a), line segment pattern (b), point pattern (c) and distance map (d). The value of the distance map (d) represent the distance to the nearest point (cm). For a detailed description see text on page 32.

Two numeric covariates were considered in addition to these spatial covariates, top height and tree density. The top height in each plot indicates environmental conditions because the height of mangrove trees is highly responsive to porewater salinity and hence an indicator of environmental stress factors (Peters et al., 2014; Vovides et al., 2014). Top height refers usually to the average height of a certain number of trees with the largest diameter (West, 2009). Instead of a fixed number of trees, I calculated the average height of the 10% trees with the largest diameter because the number of trees varied highly among plots. It was not possible to measure porewater salinity directly due to the difficulty of collecting uncontaminated soil samples in dried-out mudflat. Tree density, i.e. the number of trees in each plot, is a model term included in order to account

for propagule provision relatively to the number of trees. These two numeric covariates, top height and tree density, corresponded to one value in each plot and were spatially independent. A correlation between the numeric covariates and the spatial covariates, stem distance, crown cover and crown edge distance, is unlikely.

All covariates utilized for each point process model represent only the situation in 2011, that is the first measurement phase. I did not include any covariates measured in 2014 in order to establish an accurate causal relationship between the described biotic covariates (Table 2.1) and seedling establishment as well as tree recruitment. This includes also to understand how trees, which were already present in 2011, influenced the distribution of recruited trees, which were established between 2011 and 2014.

AREA-INTERACTION RADIUS

Although the Gibbs process algorithm is capable of fitting regular parameters θ , such as the area-interaction parameter η , irregular parameters, such as the area-interaction radius r , have to be set prior to the model fitting. Instead of choosing an area-interaction radius r which corresponds to the mean horizontal tree crown extent (Berger et al., 2008), the optimal area-interaction radius r was estimated by finding the value of radius r which resulted in the best model fit while keeping all other parameters stable (Baddeley and Turner, 2000). Statistical methods are not available to derive the AIC of point processes which contain an interaction component. Instead the pseudolikelihood was used as an indicator of model fit. The maximum pseudolikelihood indicates the relatively best fit of a model (ibid.). The optimal area-interaction radius r of each recruited tree was estimated separately for the three forest plots 1A, 1B and 2A. The area-interaction component was only included in the tree recruitment model because seedlings are not known to impact the position of neighboring seedlings.

MULTIPLE POINT PATTERNS

Point patterns are considered to be independent realizations of point processes within a bounded observation window. Consequently, replicated point patterns are considered to be multiple realizations of the same point process (Baddeley, 2013). The Gibbs fitting algorithm was used to fit a point process model to each of the three types of observed point patterns. For example, three seedling point patterns generated from mappings of three forest plots located in the same low-density forest stand were regarded as replicated observations of the same underlying ecological processes, such as the effect of herbaceous ground vege-

tation on the density of *A. germinans* seedlings. I similarly fitted two Gibbs models to point patterns of seedlings in high-density forest stands and point patterns of recruited trees. The goal was to fit one point process model which explains the distribution of seedlings or recruited trees in three forest plots and to reduce the model variance. Ecological processes which were not considered during the analysis could be revealed by analyzing the goodness-of-fit of this point process model to each observed forest plot. Additional unknown processes could be indicated if the residual error between simulated and observed point pattern follows a certain structure (McIntire and Fajardo, 2009). For example, if the effect of a certain environmental factor on tree density is stronger in one forest plots compared to other plots then it could be concluded that an unknown condition influences tree density and interacts with the measured environmental factor.

2.2.2 MODEL EVALUATION

GOODNESS-OF-FIT ANALYSIS

After selecting the best fitting model based on its AIC, the model's goodness-of-fit was evaluated based on Pearson residuals, which are obtained by dividing the raw residual value (*observed point density - predicted point density*) by the square root of observed point density (Baddeley et al., 2005):

$$\text{Pearson residual value} = \frac{\text{observed point density} - \text{predicted point density}}{\sqrt{\text{observed point density}}}$$

Pearson residuals have the mean value 0. Positive residual values indicate a density under-estimation, whereas negative values indicate over-estimation. Subsequently, the residual measures of all point were spatially interpolated or kernel smoothed to visualize the residual distribution in each forest plot and to identify possible spatial trends (Baddeley, 2008).

The goodness-of-fit of each point process model was also evaluated by comparing the observed distribution of recruited trees with simulated realizations of each point process model based on the pair-correlation function $g(r)$. The pair-correlation function $g(r)$ is a distance-dependent correlation function based on point-to-point distances and describes the density of points at a given radius r from a discrete point (Wiegand and Moloney, 2004)

$$g(r) = \frac{K'(r)}{2\pi r} \quad (2.5)$$

where $K'(r)$ is the derivative of Ripley's K -function $K(r)$ which is the expected standardized number of neighboring trees in a circle of radius r around a focal tree (ibid.). The boundaries of the 199 Monte Carlo simulation envelopes were

formed by the fifth-highest and the fifth-lowest values resulting in a significance level $\alpha = 0.05$ (Baddeley et al., 2014). A departure of the observed point pattern distribution from the simulated envelope would indicate a lack of fit.

SENSITIVITY ANALYSIS

The sensitivity of each model was evaluated with leverage and influence diagnostic tools developed by Baddeley et al. (2013). The leverage function enabled me to screen the fitted models for influential covariates, whereas the results of the influence analysis indicated potential outliers within the point pattern.

The leverage value $h(u)$ at location u corresponds to the magnitude the fitted model would have changed if a point would have been mapped at the location u relatively to other areas. High leverage values indicate the presence or values of covariates, e.g. environmental factors, which could have a high influence on the intensity of the fitted point process model. In this study, high levels of leverage indicated a strong influence of a spatial covariate on the density of seedlings and trees.

The influence value $s(x_i)$ at a mapped point x_i corresponds to the magnitude the fitted model would have changed if this particular point x_i would be deleted. High influence values indicate mapped points which have a large influence on the fitted model and are potential outliers.

Both sensitivity diagnostics, leverage and influence values, are only applicable to Poisson point process models and cannot be used for models which contain interpoint interactions $C(u, x)$. To close this gap, quantile-quantile plots (Q-Q plots) and the pair-correlation function $g(r)$ were used to compare the fit of the point process model without interaction component, i.e. a Poisson point process, and the model with an area-interaction model to the observed tree recruitment pattern.

In the context of linear regression, Q-Q plots are usually applied to check the normal distribution of errors. Similarly, Q-Q plots can be used to check the distributional assumption of a point interaction model and compare the appropriateness of different interaction models. The quantiles of the observed smoothed Pearson residuals are plotted against the quantiles of the theoretically expected Pearson residuals, which were estimated based on 100 simulations (Baddeley et al., 2005).

The R package spatstat (version 1.40-0) was employed for model-fitting and model evaluation (Baddeley and Turner, 2005).

2.3 RESULTS

2.3.1 DESCRIPTIVE RESULTS

In 2011, the forest plots 1A, 1B and 2A were characterized by very low tree and seedling densities (Figure 2.5a). Between 2011 and 2014, tree density increased by a factor of 4, in 2A, to 8, in 1A. Furthermore, seedling density increased 20- to 35-times in these plots. In plot 1A and 1B, seedling density was either lower (2011) or equal (2014) to tree density. Although tree and seedling density increased, the tree height distribution did not change between 2011 and 2014. Only in plot 1A, the height of the tallest trees increased (Figure 2.5b). The height distribution of the top trees of 3A and 3B was different to the other plots. The increase in tree density was positively associated with an increase of canopy cover (Figure 2.5c).

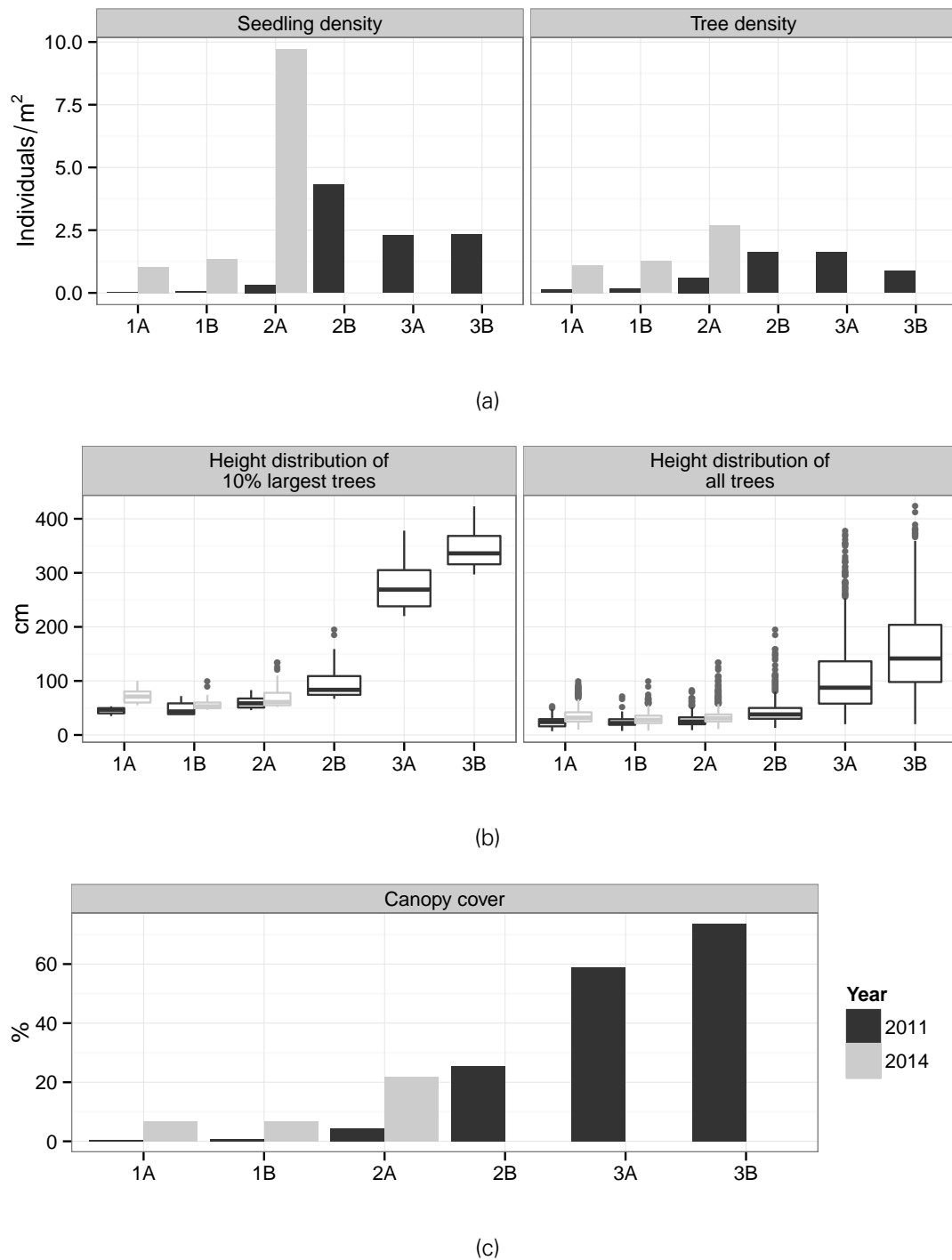


Figure 2.5: Comparison of stand structure in the forest plots 1A to 3B in 2011 (black). The plots 1A to 2A were remeasured in 2014 (grey). The structural description includes (a) seedling and tree density, (b) tree height distribution of largest 10% and all trees, and (c) canopy cover.

The coverage of herbaceous salt-marsh vegetation was mapped only in 2011. In plot 3A, 60% of the forest floor was covered by herbaceous vegetation, in all other plots herb coverage was below 20% (Figure 2.6). *S. portulacastrum* was found in 1A to 2B where it formed small patches throughout the plot area. *B.*

portulacoides was mainly found in 3A and 3B where it covered large continuous areas (Figure 2.8). The area where the patches of two salt-marsh species overlapped was negligible ($< 0.1\%$) and thus excluded from the following analysis.

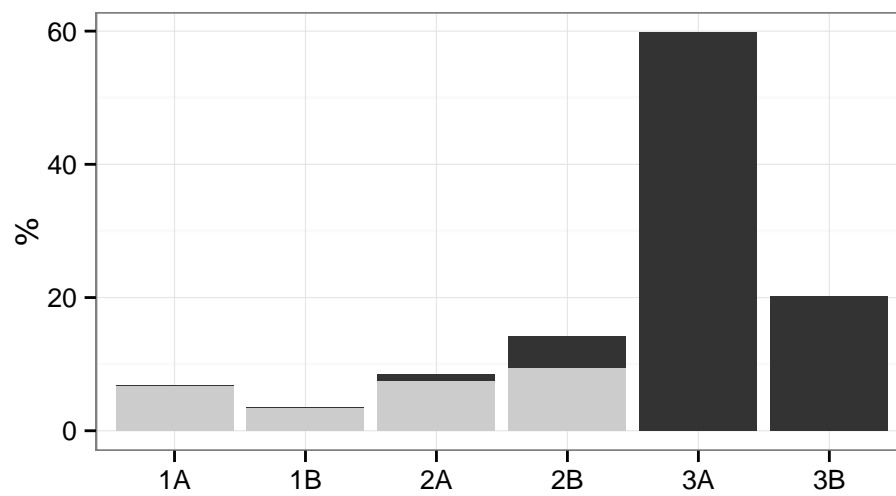


Figure 2.6: Coverage of the salt-marsh herb species *B. portulacoides* (black) and *S. portulacastrum* (grey) in each forest plot in 2011.

Figure 2.7 indicates that seedling density could be higher under or in close proximity to tree crowns.

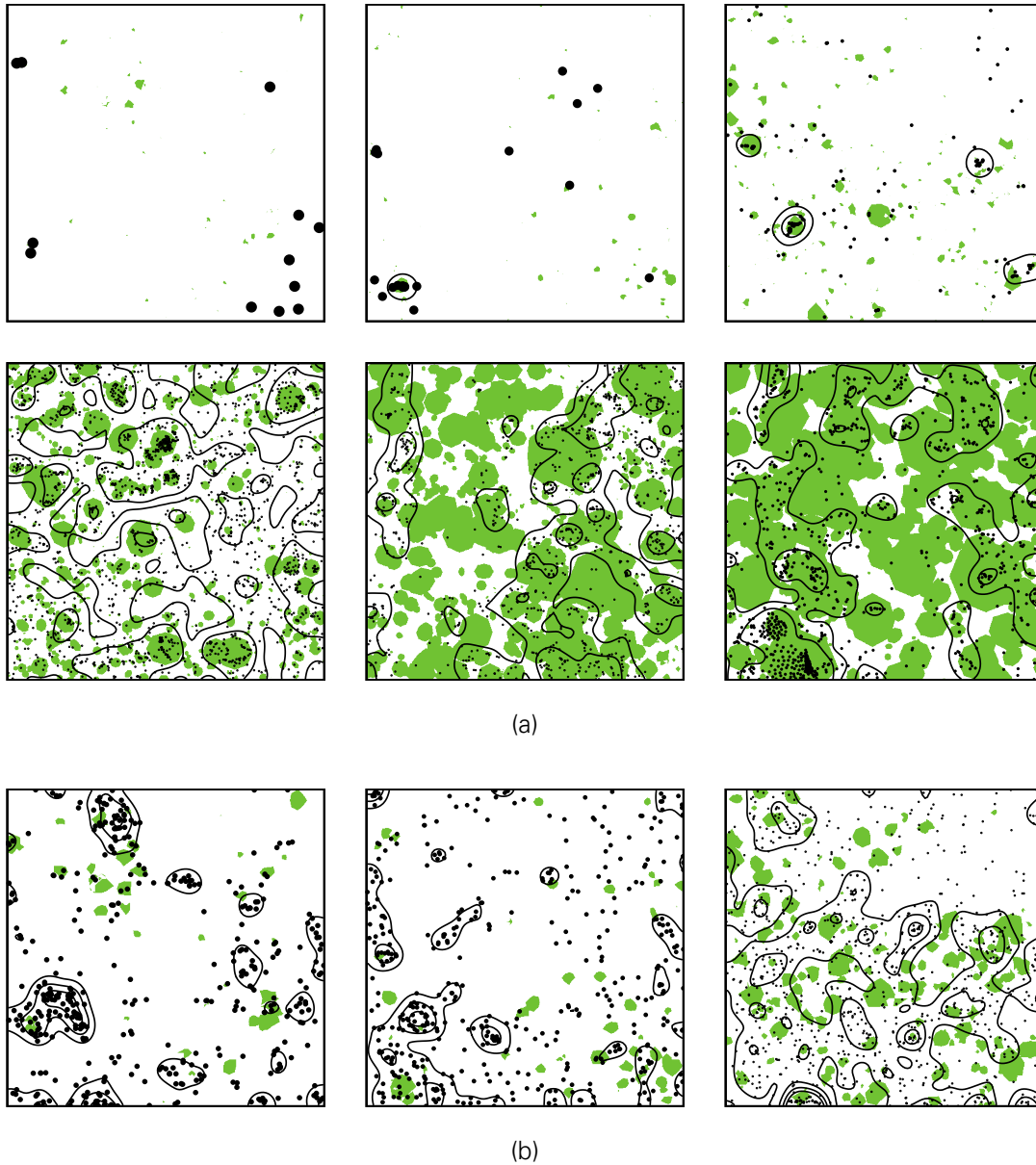


Figure 2.7: The spatial variation plots of (a) seedlings superimposed over canopy cover (green) in 2011 and (b) tree recruits superimposed over canopy cover of non-recruited trees (green) in 2014. Solid lines show the smoothed intensity of seedling pattern. Individual points are sized proportional to the total density in order to ease visual interpretation. In (a), plots in the low-density forest stand (1A, 1B and 2A) are placed in the top row from left to right and plots in high-density stand (2B, 3A and 3B) are placed in the bottom row from left to right. All plots in (a) were mapped in 2011. In (b), plots 1A, 1B and 2A (mapped in 2014) are placed from left to right.

Figure 2.8 shows the distribution of *A. germinans* seedlings and recruits as well as the distribution of the succulent plants *Sesuvium portulacastrum* and *Blutaparon portulacoides* in the study site.

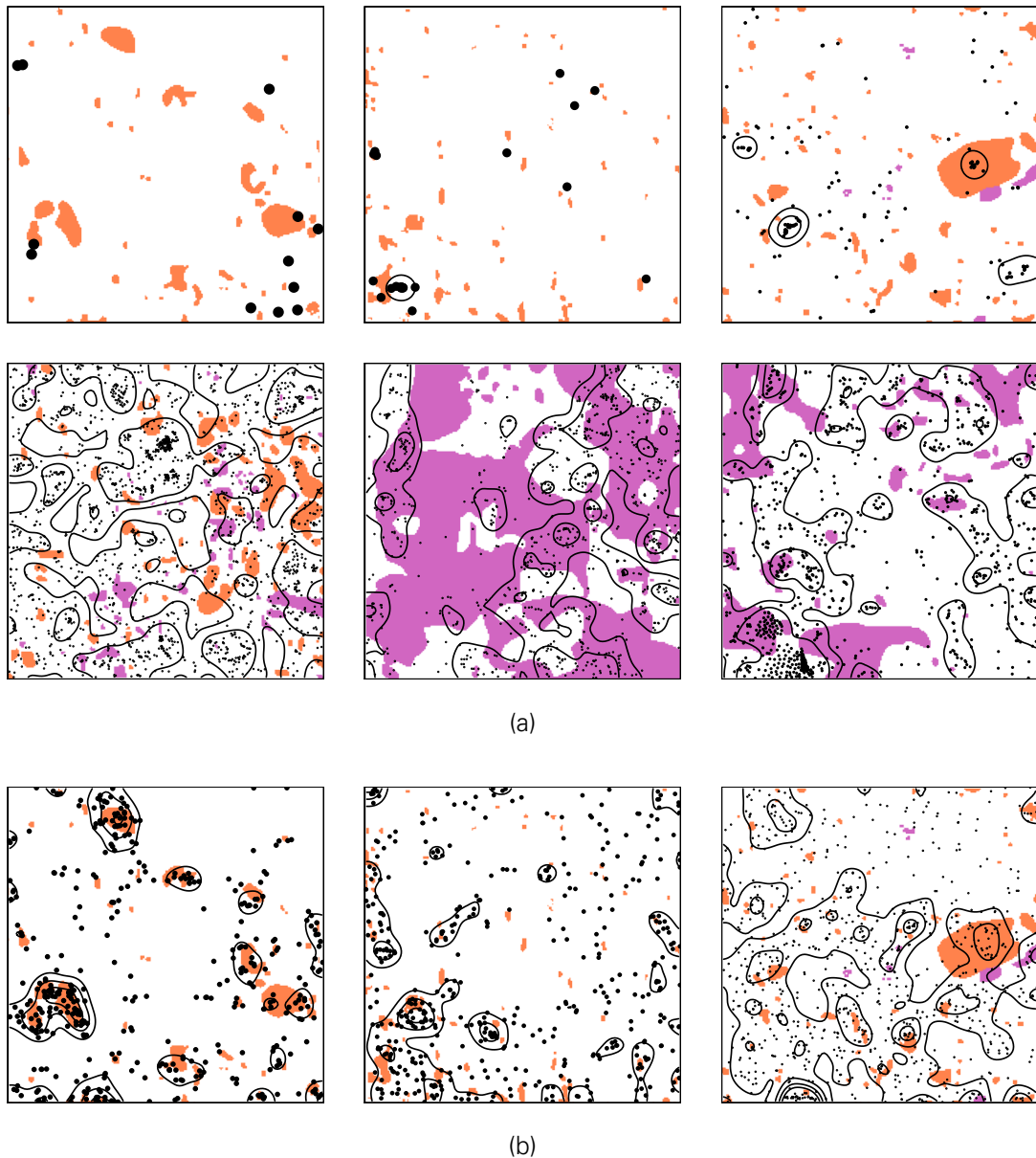


Figure 2.8: The spatial variation plots of (a) seedlings and (b) tree recruits superimposed over *S. portulacastrum* (orange) and *B. portulacoides* (purple). Solid lines show the smoothed intensity of seedling pattern. Individual points are sized proportional to the total density in order to ease visual interpretation. In (a), plots in the low-density forest stand (1A, 1B and 2A) are placed in the top row from left to right and plots in high-density stand (2B, 3A and 3B) are placed in the bottom row from left to right. All plots in (a) were mapped in 2011. In (b), plots 1A, 1B and 2A are placed from left to right. Recruited trees were mapped in 2014.

Remaining logs of the pre-disturbance forest stand are scattered across the site (Figure 2.9).

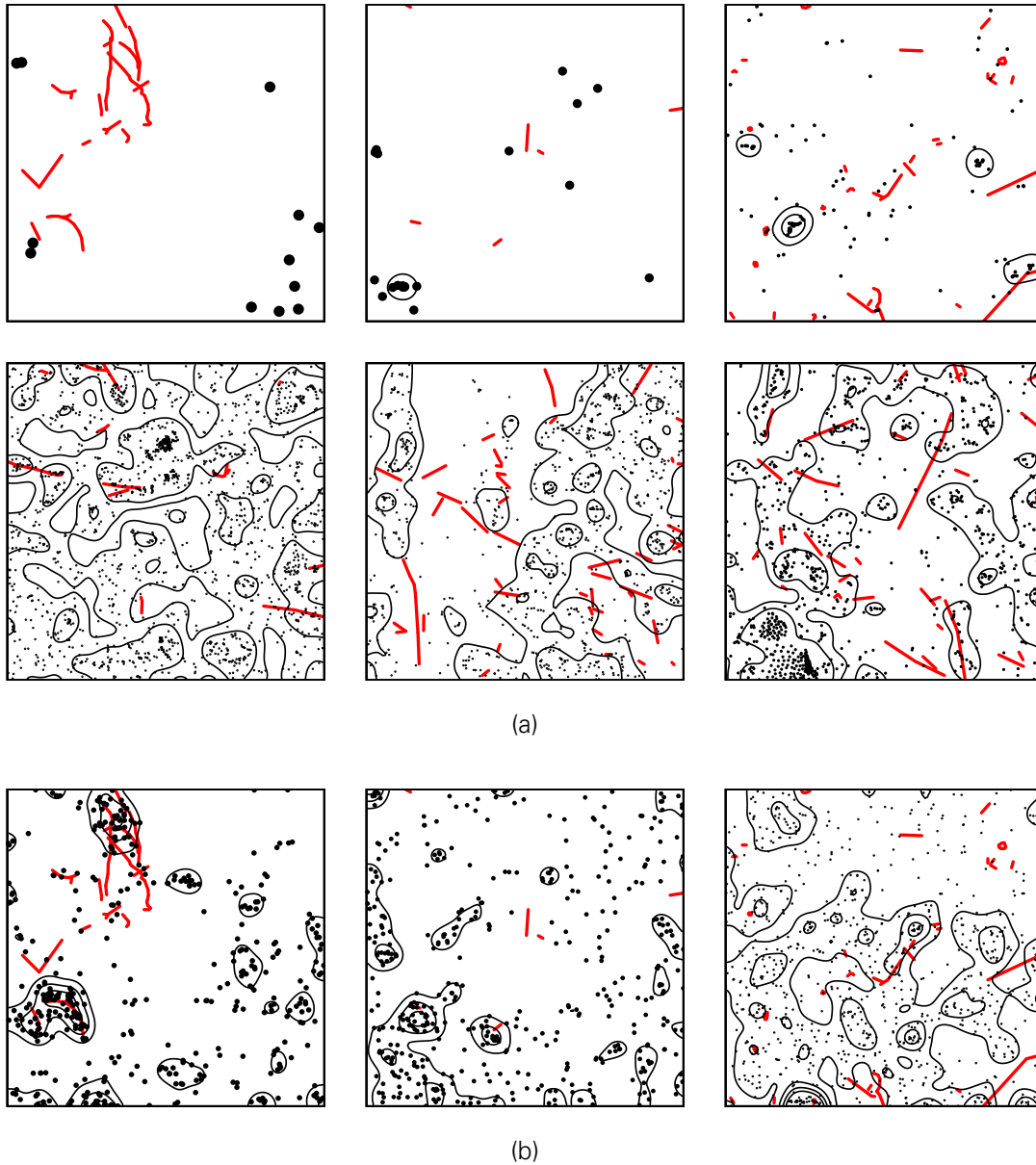


Figure 2.9: The spatial variation plots of (a) seedlings as well as (b) tree recruits superimposed over wood debris segments (red lines). Solid black lines show the smoothed intensity of seedling pattern. Individual points are sized proportional to the total density in order to ease visual interpretation. In (a), plots in the low-density forest stand (1A, 1B and 2A) are placed in the top row from left to right and plots in high-density stand (2B, 3A and 3B) are placed in the bottom row from left to right. All plots in (a) were mapped in 2011. In (b), plots 1A, 1B and 2A are placed from left to right. Recruited trees were mapped in 2014.

2.3.2 SEEDLING ESTABLISHMENT

By step-wise forward model selection, I selected the best-fitting point process model for seedling establishment in forest stands with low (plot 1A to 2A) as well as high tree density (2B to 3B). The estimates for the parameters of each model are listed in Table 2.2.

In the model for seedling establishment in low-density forest stands (Table 2.2a), top height and the distance to nearest tree had no significant influence and were excluded. The model term 'crown cover' was more significant and resulted in a better fitting model than the distance to the nearest crown edge ('crown edge distance'). Hence, model LD3 was the most appropriate model to describe the observed seedling distribution. Seedling density is much higher under the crown cover of trees. The positive effect of crown cover is greater in stands with low tree density.

In the high-density stands all three tree-related model terms were significant (Table 2.2b). Based on its low AIC value, model HD3 describes seedling establishment best. Seedling density is negatively related to the distance to the nearest crown edge, indicating that more seedling are established adjacent or underneath tree crowns. Figure 2.10 shows the relationship between tree crown and seedling density in more detail. In all plots most seedlings are found under the crown of trees, i.e. distance to crown edge = 0 cm. The maximum distance between crown edge and seedling position declines with increasing tree density.

The positive effect of *S. portulacastrum* cover on seedling density was slightly significant in the model LD3 (p -value < 0.05), whereas seedling density was more significantly related to *B. portulacoides* cover in HD3 (p -value < 0.001). Thus, in both forest stands seedling density was higher in herb patches of *S. portulacastrum* and *B. portulacoides* in contrast to adjacent bare areas. Distance to wood debris was excluded from all models because it did not improve the fit of the point process models based on the AIC.

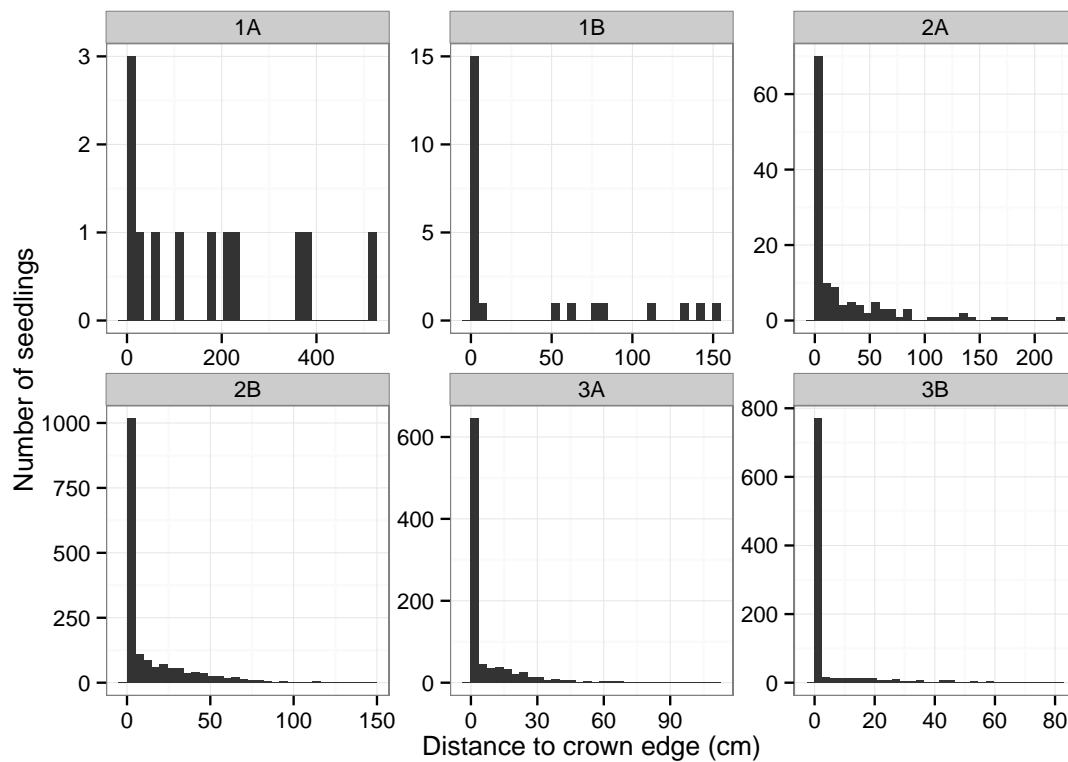


Figure 2.10: Number of seedlings in relationship to the distance to the nearest crown edge. A distance of 0 cm is associated with the crown edge as well as crown cover.

Figure 2.11 shows the distribution of residual values, i.e. the difference between observed and predicted seedling density. In general, the deviation of the model from the observed seedling distribution is relatively small. Seedling establishment was underestimated only in corner areas of plot indicating the influence of trees located outside the plot. The model for seedling establishment in low-density stands is particularly sensitive to the covariates 'crown cover' and 'distance to nearest tree' because leverage values correspond to tree proximity and large crown areas. Thus, this model is particularly sensitive to tree proximity and crown area which is in accordance with the estimated parameters (Figure 2.12, top). On the other hand, seedlings which were located within herb patches had the strongest influence on this first model of seedling establishment (Figure 2.13, top).

Table 2.2: Parameter estimates for stepwise forward fitted Gibbs point process model of seedling establishment in forest stands of low (a, model LD) and high tree density (b, model HD). Each Model LD was fitted to multiple point patterns from plot 1A, 1B and 2A, whereas each Model HD was fitted to multiple point patterns from plot 2B, 3A and 3B. The corresponding standard errors are presented in brackets. The lowest AIC-value is highlighted in bold. See Table 2.1 for a detailed description of all model parameters.

	Model LD1	Model LD2	Model LD3
Intercept	-13.2478*** (0.6227)	-10.9154*** (1.3220)	-13.2376*** (0.3639)
Tree density	0.0120*** (0.0028)	0.0070 (0.0051)	0.0090*** (0.0017)
<i>S. portulacastrum</i>	0.7235 (0.5582)	0.3429 (0.9974)	0.6495* (0.3269)
<i>B. portulacoides</i>	-12.9785 (884.7763)	-13.1156 (1544.4697)	-13.2721 (852.1925)
Crown edge distance		-0.0153* (0.0078)	
Crown cover			3.1435*** (0.2385)
AIC	30733.31	2977.12	2849.51
Note:	*p<0.05; **p<0.01; ***p<0.001		

(a)

	Model HD1	Model HD2	Model HD3	Model HD4
Intercept	-6.8494*** (0.2976)	-5.9868*** (0.3106)	-5.8472*** (0.2994)	-6.7002*** (0.2887)
Top height	-0.004*** (0.0005)	-0.0043*** (0.0005)	-0.0062*** (0.0005)	-0.0063*** (0.0005)
Tree density	-0.0008* (0.0004)	-0.0014*** (0.0004)	-0.0013*** (0.0004)	-0.0012*** (0.0004)
<i>S. portulacastrum</i>	-0.2058 (0.1515)	-0.1786 (0.1502)	0.0861 (0.1507)	0.0028 (0.1489)
<i>B. portulacoides</i>	0.1047 (0.0829)	0.1511 (0.0832)	0.284*** (0.0825)	0.3276*** (0.0815)
Tree stem distance		-0.0103*** (0.0012)		
Crown edge distance			-0.02*** (0.0016)	
Crown cover				0.9029*** (0.0654)
AIC	52399.34	52196.83	51933.85	51944.67
Note:	*p<0.05; **p<0.01; ***p<0.001			

(b)

The residual analysis of the model for seedling establishment in high-density stands revealed positive residuals, i.e. under-estimation of seedling densities, around one tree group in the central plot area, and an elongated area of negative value, i.e. over-estimation, which are possibly explained by a ridge area which hinders propagule dispersal. Both leverage (Figure 2.12, bottom) and influence function (Figure 2.13, bottom) suggest that this model is most sensitive to areas of the herb *S. portulacastrum* which only occurs in plot 2B.

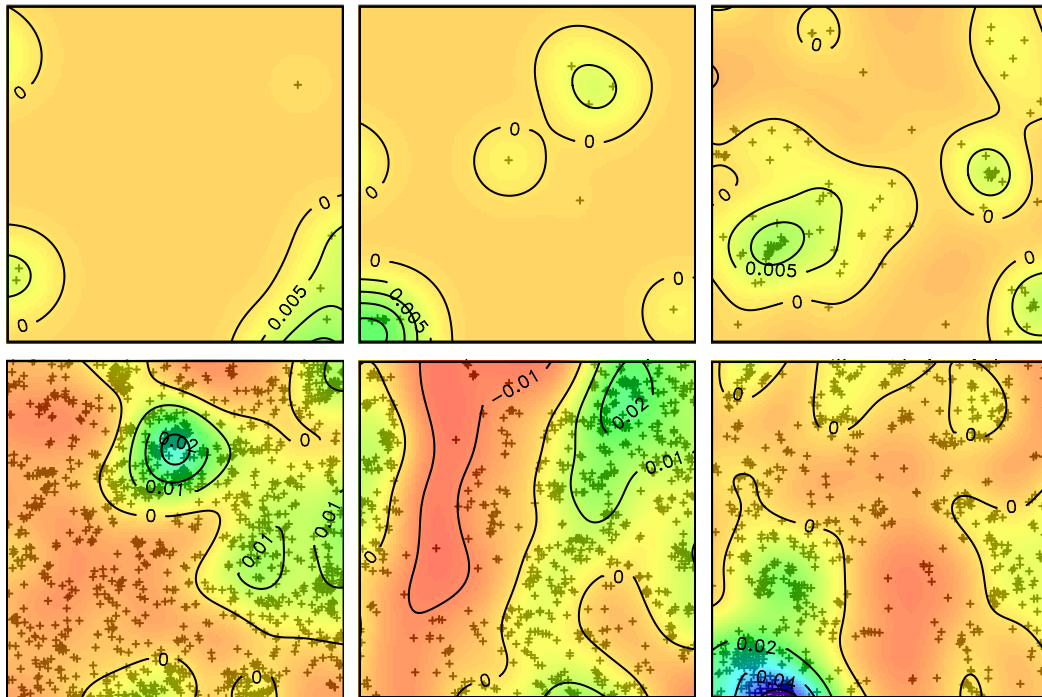


Figure 2.11: Residuals of fitted seedling model superimposed on seedling positions (+) within observation window (18 m x 18 m) after trimming 1 m off each plot border. Residual values range from -0.015 to 0.09. Positive residual values indicate an under-estimation of seedling density, whereas negative values indicate an over-estimation. Plots in low-density stand (1A, 1B and 2A) in the top row from left to right and plots in high-density stand (2B, 3A and 3B) in the bottom row from left to right.

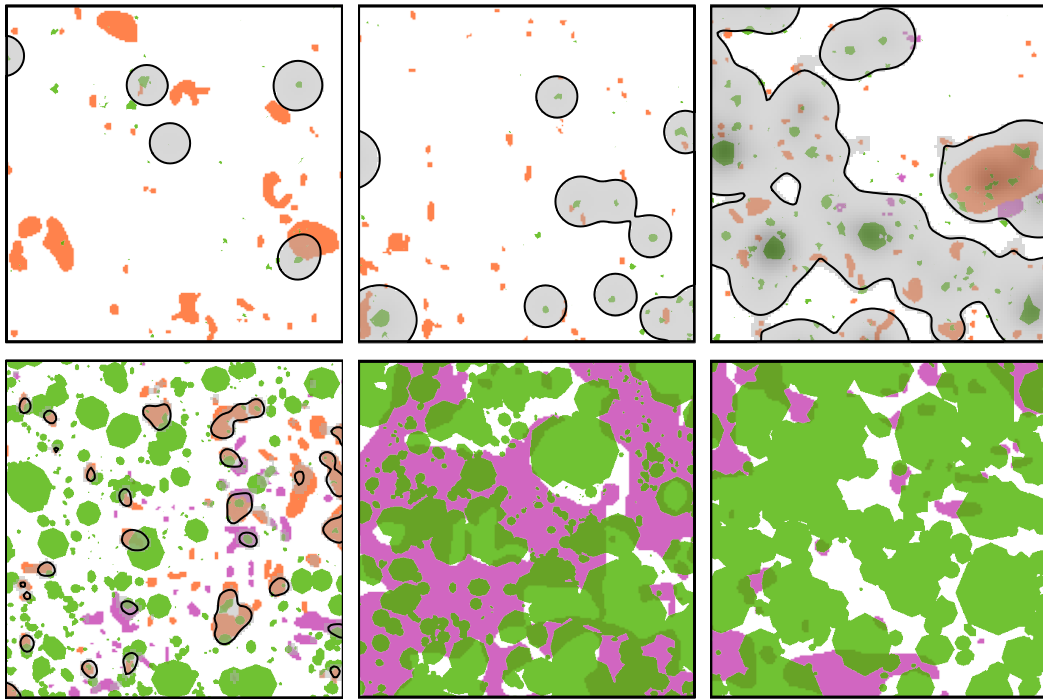


Figure 2.12: Leverage function of fitted seedling model as grey-scale images with contour at mean leverage value superimposed over a map of crown area (green), *S. portulacastrum* (orange) and *B. portulacoides* (purple) within the observation window (18 m x 18 m) after trimming 1 m off each plot border. Leverage values range from 0 to 0.00012. Plots in low-density stand (1A, 1B and 2A) in the top row from left to right and plots in high-density stand (2B, 3A and 3B) in the bottom row from left to right. High leverage values indicate the presence or values of covariates, which could have a high influence on the intensity of the fitted point process model.

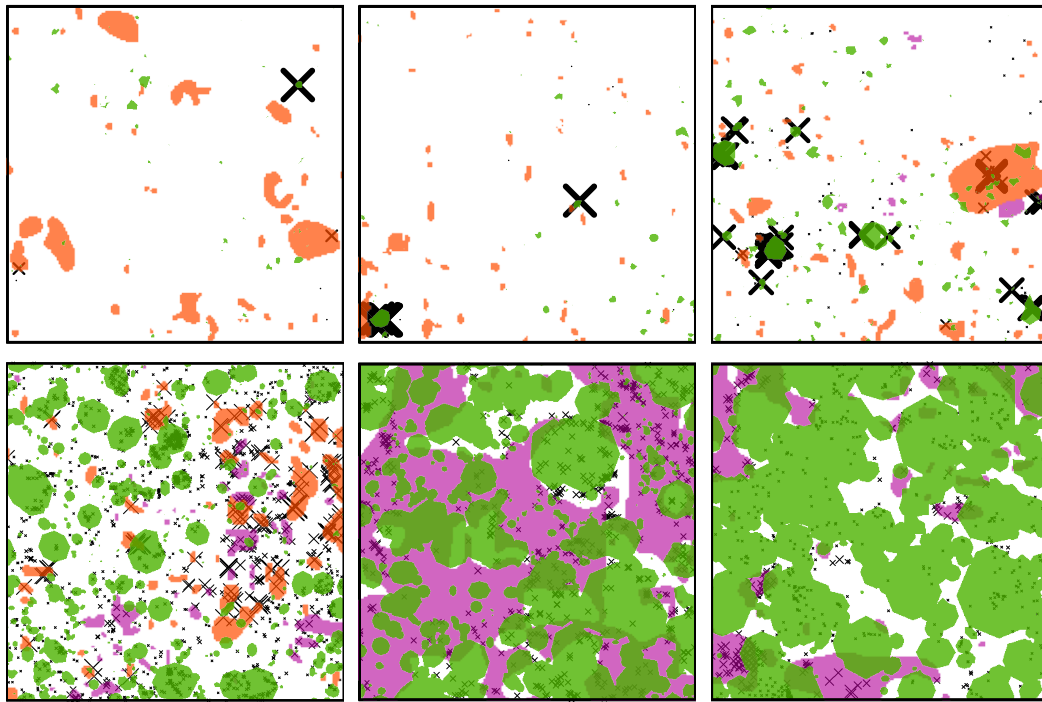


Figure 2.13: Influence function of fitted seedling establishment model superimposed over a map of crown area (green), *S. portulacastrum* (orange) and *B. portulacoides* (purple) within observation window (18 m x 18 m) after trimming 1 m off each plot border. The size of each cross (x) is proportional to the influence measure s_i of the seedling on the model. High influence values (larger crosses) indicate mapped points which have a high influence on the fitted model. Plots in low-density stand (1A, 1B and 2A) in the top row from left to right and plots in high-density stand (2B, 3A and 3B) in the bottom row from left to right.

2.3.3 TREE RECRUITMENT

I analyzed which factors influence the distribution of trees which were mapped only in 2014 (Table 2.3). That means that these trees were established only within three years.

I first analyzed the influence of trees which already existed in 2011, so called non-recruited trees, on the density of tree recruitment between 2011 and 2014. I compared how the tree crown extent in 2011 and 2014 of these older trees influenced recruitment. On the one hand, I found that the tree crown in 2011 had no significant influence on subsequent tree recruitment. On the other hand, the crown area in 2014 of non-recruited trees had a significant influence on previously occurring tree recruitment. Although recruitment was denser in close proximity to the crown edge of non-recruited trees in 2014, nearest tree stem distance was a better predictor of tree recruitment density according to the

lower AIC. Thus, tree recruitment significantly decreased with distance to the nearest non-recruited tree. Moreover, the tree density in 2011 was significantly positive related to the tree density in 2014.

The Gibbs point process models also allow the analysis of interactions among recruited trees. I used an area-interaction model with a radius estimated based on finding the radius r which resulted in the best model-fit. The results indicate that recruited trees are clustered within a radius of 31, 37 and 14 cm in plot 1A, 1B and 2A respectively (Figure 2.14). The area-interaction value η of 2.5 revealed that recruits cluster strongly within these areas after accounting for other environmental conditions. Factors related to non-recruited trees became of small significance after I included the area-interaction model. After including the interaction component, the AIC cannot be extracted because the model is no longer a Poisson process model.

The negative model parameters North and West indicate that there is a very small gradient of declining recruitment from NW to SE. Considering its effect size, *S. portulacastrum* was the most important spatial covariate for tree recruitment. Interestingly, the herb *S. portulacastrum* has a strong positive influence on the recruitment of trees. That means that we found significantly more recruited trees in former herb patches.

Table 2.3: Parameter estimates for stepwise forward fitted Gibbs fitted point process model of tree recruitment (model TR). The corresponding standard errors are presented in brackets. The model terms 'North' and 'West' indicate a spatial trend corresponding to these directions. 'Tree density of non-recruited trees' refers to the number of trees in 2011. 'Distance to nearest tree stem' refers to the distance to the nearest stem of a tree which has not been recruited within the time period between 2011 and 2014 (non-recruited tree). 'Distance to nearest crown edge' refers to the crown edge of non-recruited trees in 2014. Each Model TR was fitted to multiple point patterns from plot 1A, 1B and 2A. See Table 2.1 for a detailed description of all model parameters.

	Model TR1	Model TR2	Model TR3	Model TR4
Intercept	-9.6318*** (0.1301)	-9.2288*** (0.1503)	-9.219*** (0.1243)	-10.5068*** (0.1559)
North	-0.0004*** (0.0001)	-0.0004*** (0.0001)	0.0003*** (0.0001)	-0.0002** (0.0001)
West	-0.0005*** (0.0001)	-0.0004*** (0.0001)	-0.0005*** (0.0001)	-0.0002** (0.0001)
Tree density of non-recruited trees	0.0046*** (0.0004)	0.0035*** (0.0005)	0.0033*** (0.0004)	0.0071*** (0.0005)
<i>S. portulacastrum</i>	0.9558*** (0.1053)	0.8610*** (0.1067)	0.8665*** (0.0958)	0.4383*** (0.1005)
<i>B. portulacoides</i>	0.3127 (0.5662)	0.2009 (0.5658)	0.7772*** (0.3728)	0.0071 (0.5231)
Distance to nearest stem of non-recruits		-0.0027*** (0.0006)		-0.0014* (0.0005)
Distance to nearest crown edge of non-recruits			-0.0008*** (0.0004)	
Area-Interaction η				2.5116*** (0.1059)
AIC	26240.18	26195	26210.55	NA
Note:		*p<0.05; **p<0.01; ***p<0.001		

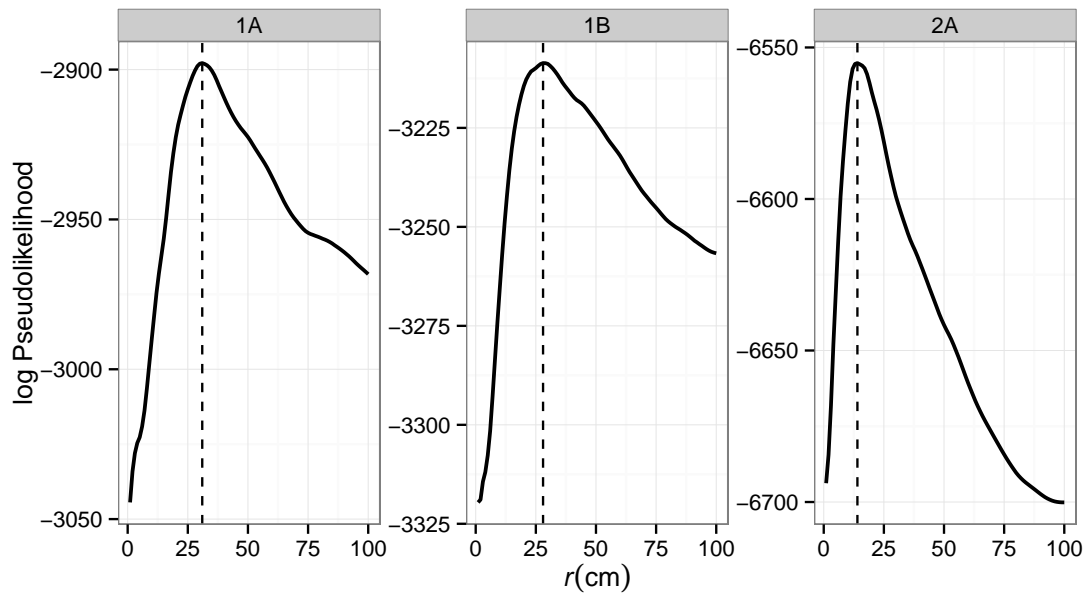


Figure 2.14: Estimation of the optimal area-interaction radius r around each recruited tree by finding the area-interaction radius r which results in the best-fitting Gibbs point process model based on the maximum pseudolikelihood (dashed line).

Figure 2.15 shows areas of underestimated tree density (positive residual values) and overestimated tree density (negative residual values) which correspond to patches of salt-marsh vegetation and areas without herb vegetation cover respectively. The leverage (Figure 2.16) and influence analysis (Figure 2.17) show that both herb species had a high influence on the fitted recruitment model. *B. portulacoides* patches in plot 2A display the highest leverage values. Trees mapped in these herb patches are most influential on the model.

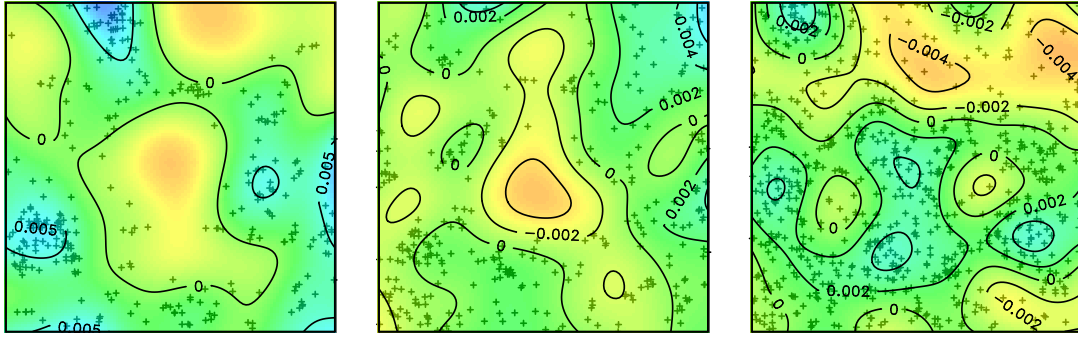


Figure 2.15: Residuals of the fitted recruitment model superimposed on position of recruited trees (+) within the observation window (18 m x 18 m) after trimming 1 m off each plot border (plot 1A, 1B and 2A from left to right). Residual values range from -0.008 to 0.02. Positive residual values indicate an under-estimation of tree recruits density, whereas negative values indicate an over-estimation.

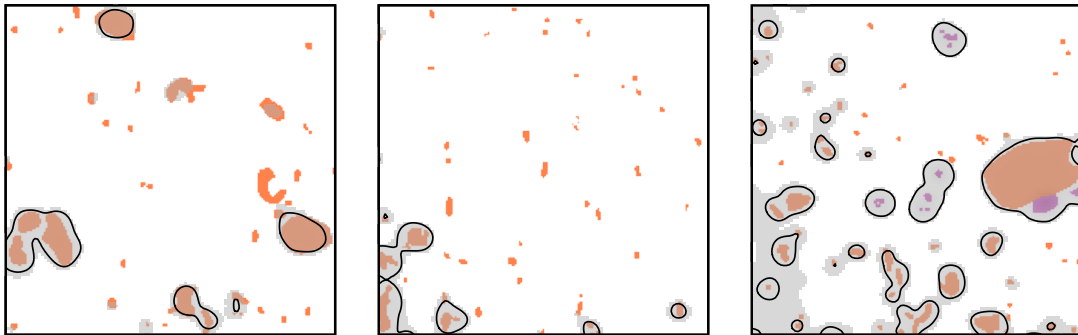


Figure 2.16: Leverage function of the fitted recruitment model without area-interaction (Model TR2) as grey-scale images with contour at mean leverage value superimposed over *S. portulacastrum* (orange) and *B. portulacoides* (purple) within the observation window (18 m x 18 m) after trimming 1 m off each plot border (plot 1A, 1B and 2A from left to right). Leverage values range from 0 to 0.00008. High leverage values indicate the presence or values of covariates, which could have a high influence on the intensity of the fitted point process model.

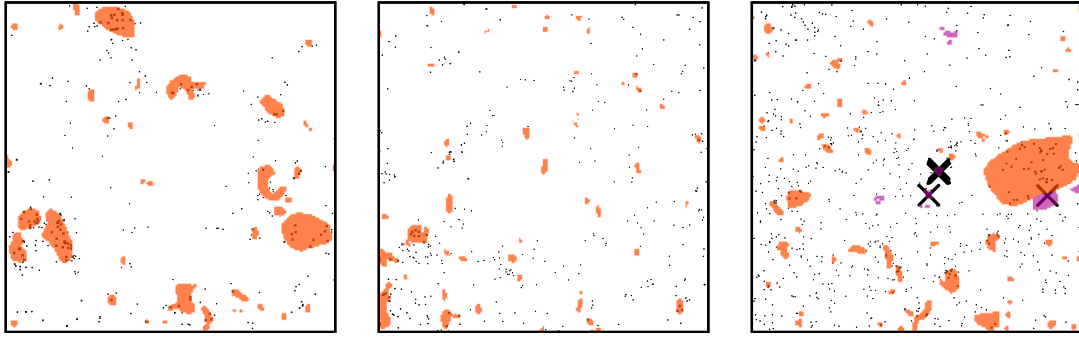


Figure 2.17: Influence function of the fitted recruitment model without area-interaction (Model TR2) superimposed over *S. portulacastrum* (orange) and *B. portulacoides* (purple) within the observation window (18 m x 18 m) after trimming 1 m off each plot border (plot 1A, 1B and 2A from left to right). The size of each cross (x) is proportional to the influence measure s_i of the recruited trees on the model. High influence values (larger crosses) indicate mapped points which have a high influence on the fitted model.

Figure 2.18 shows Q–Q plots for Poisson (TR2) and area-Interaction model (TR4) fitted to each plot from 100 simulated realizations of the fitted model. Overall, the area-interaction model suggest a better agreement between the fitted point process model and the mapped recruit distribution.

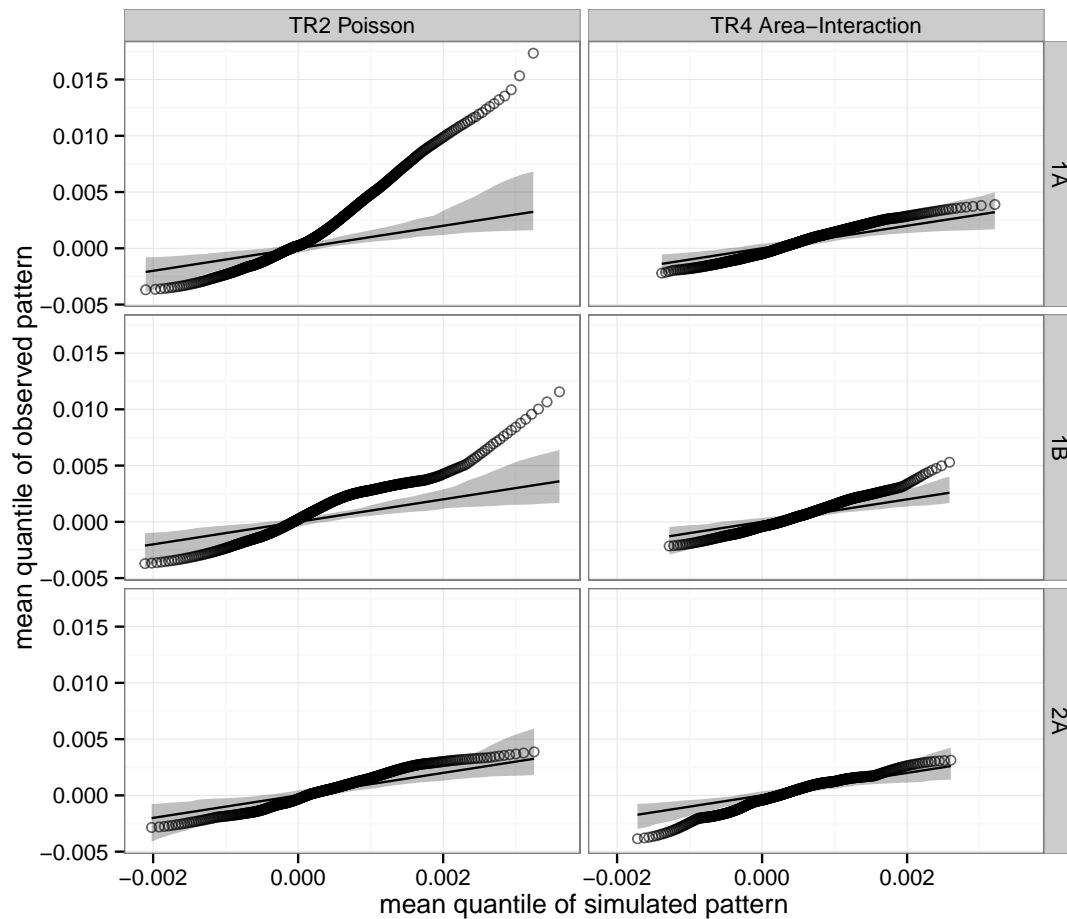


Figure 2.18: Quantile-quantile plot (Q-Q plot) of the observed Pearson residuals of the point process models for tree recruitment without (Model TR2) and with area-interaction process (Model TR4) in relation to the mean quantiles of 100 simulations (solid line). Grey bands indicate 95% simulation envelopes.

In addition to Q-Q plots, pair-correlation functions $g(r)$ of the simulated point process models were generated in order to assess the fit of each point process model to the observed recruitment pattern (Figure 2.19). The better fit of the simulation envelope based on the area-interaction model TR4 to the observed point pattern compared to the Poisson model TR2 showed that the area-interaction model is more appropriate similarly to the Q-Q plots. The pair-correlation values $g(r)$ of the observed recruitment point pattern was slightly higher than the simulation envelopes at a distance between 50 cm and 100 cm, which indicates that recruited trees were more clustered at this distance than suggested by the model. The pair-correlation function showed also that the observed recruited trees were clustered up to a distance of approximately 1 m in plot 1A and 1B, whereas in plot 2A clustering of recruits was limited to a distance of approximately 50 cm clusters.

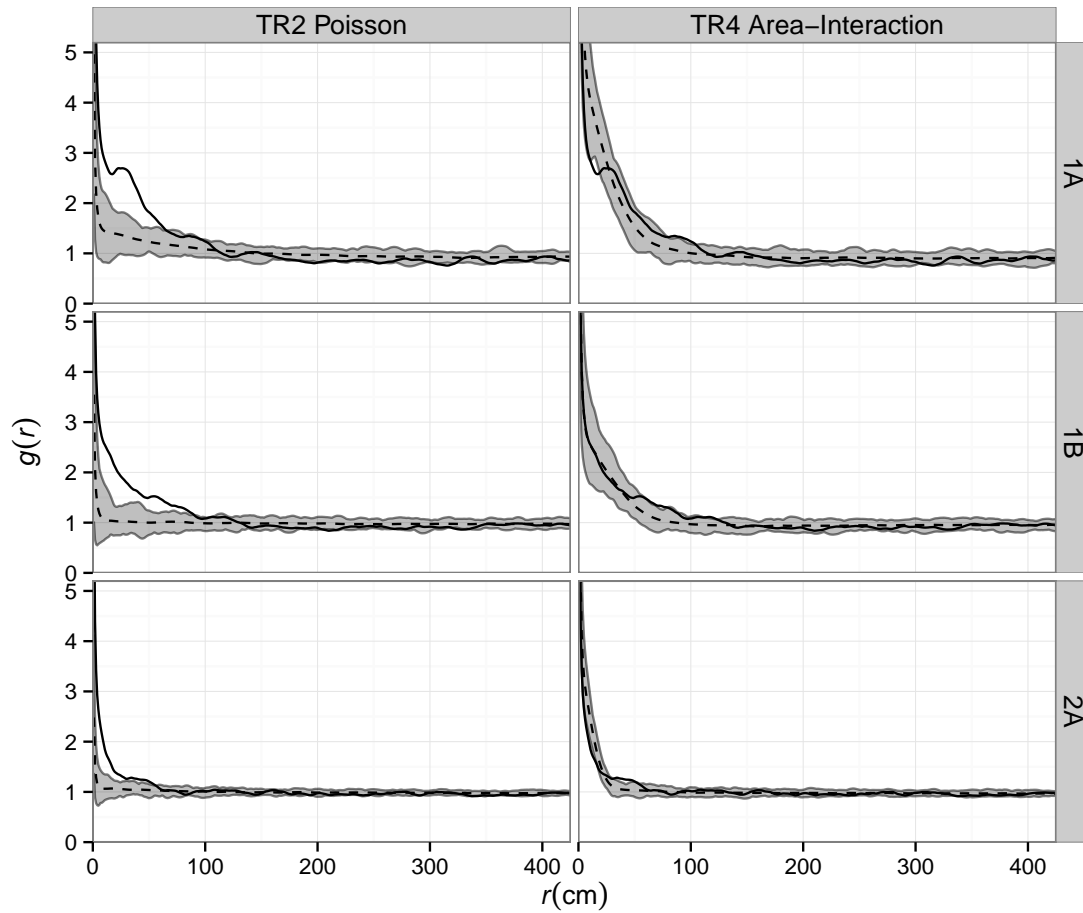


Figure 2.19: Goodness-of-fit assessment of observed spatial pattern of recruited trees to the Poisson process model TR2 and the area-interaction model TR4 based on the pair-correlation function $g(r)$. Grey bands indicate 95% simulation envelopes which are formed by the fifth-highest and fifth-lowest $g(r)$ value generated by 199 simulations of model TR2 and TR4. The dashed line delineates the theoretical value for a random distribution with the same intensity.

2.4 DISCUSSION

Recolonization is the first phase in mangrove forest development, which is followed by the mature and final senescence forest phase (Alongi, 2002; Duke, 2001; Fromard et al., 1998). Processes which take place in this first stage have great influence on the following forest development. Previous studies have shown the positive effect of mature trees, a protective canopy cover (Fajardo and McIntire, 2011) and herbaceous vegetation (McKee et al., 2007) on mangrove regeneration. However, all these factors were studied isolated from each other although they act simultaneously on mangrove propagules and seedlings. The objective of this study was to analyze the spatial dependency of *A. germi-*

nans regeneration, i.e. seedling establishment and tree recruitment, on local biotic factors during the recolonization phase following a stand-replacing event. I hypothesized that seedlings are either denser around the stem position of the nearest neighboring tree or under crown cover. Furthermore, herbaceous vegetation cover and wood debris would increase the density of seedlings as well as tree recruits. I also hypothesized that recruits are clustered.

Gibbs point process models provided the flexible framework for analyzing simultaneously the dependency of point patterns on spatial external covariates as well as the effects of inter-point interaction processes. The validity and sensitivity of each model was assessed using residual, leverage and influence diagnostic tools as well as Q-Q plots and simulation envelopes.

In addition, I applied recently developed methods which accommodate multiple point patterns replicated by similar point processes. Combining forest plots located in similar forest stands allowed me to understand the 'bigger picture' in each forest stand and to detect subtle differences within each stand through the means of residual point process analysis. These diagnostic tools were used to evaluate the appropriateness of each process model.

The results revealed that canopy cover and distance to the crown edge explained seedling establishment best both in low-density and high-density forest stands. Although seedling density was significantly higher in patches of herbaceous vegetation cover, the effect of herb plants was more substantial in the recruitment of *A. germinans* trees. Coarse wood debris had no effect on either life stage. The area-interaction process revealed that tree recruits were strongly clustered.

2.4.1 TREE VEGETATION

The point process model showed that non-recruited trees had the highest positive influence on seedling density compared to herbaceous vegetation or wood debris. However, the positive influence of tree crowns on seedling establishment was more significant than the distance to the nearest tree stems. The highest seedling density occurred directly underneath tree crowns in both low- and high-density forest stands. Inundations were infrequent and tidal currents weak, which caused seedlings to establish close by or within their parent's seed shadow. Propagules either established directly in the seed shadow, i.e. under the crown of their parent tree, or were dispersed further after landing by tides.

Propagules which land in areas outside canopy cover experience more higher temperatures and more intense sunlight resulting in higher rates of mortality (McKee, 1995b). These environmental stress factors could be ameliorated by

trees acting as nurse plants and reducing seedling mortality (Vogt et al., 2014). Therefore, this spatial pattern could not only be the result of seed dispersal processes (for more details see chapter 4).

Trees in the low-density forest stand were very small in size, on average 25 cm tall, but produced propagules (own observation). The aggregation of seedlings around trees is evidence that trees are too small to interfere with seedling establishment by reducing sunlight. In plot 1A (2011), the position of seedlings was less associated with trees which indicates that trees inside the plot only produced a small amount of propagules, whereas the majority originated from external sources.

Tree height was either not significantly associated with seedling density in low density stands, or significantly negative associated in high density stands which is in contrast to my initial hypothesis. I suggest that better environmental condition not only increased height growth but also intensified competition between trees and seedlings for limited sunlight. The overall negative relationship of seedling density and tree density provides more evidence for this explanation. Therefore, more propagules may be produced as tree density increases, but seedlings lack the required solar radiation to grow and survive.

I used tree height as an indicator of environmental conditions because tree height is limited by hypersalinity (Peters et al., 2014; Vovides et al., 2014). I hypothesized that higher top tree height would be associated with higher seedling density because it would reflect better site conditions. The negative relation of top height and seedling density in the high-density stand suggests that better site conditions increase competition between trees and seedlings. Thus, better tree growth limits the sunlight available for seedling establishment. It can be concluded that hypersalinity does not impair seedling establishment as much as limited light at ground level (López-Hoffman et al., 2007).

Non-recruited trees, i.e. trees which were already mapped in 2011, did not have a significant influence on tree recruitment in the following three years. This does not necessarily mean that non-recruited trees did not act as starting points for the recolonization of the degraded site. However, their influence on the spatial distribution of neighboring trees became less apparent as forest development progressed. Therefore, the time interval between the surveys in 2011 and 2014 was too long to observe the influence of trees on subsequent regeneration beyond the seedling life-stage.

2.4.2 INTERACTION AMONG RECRUITED TREES

I included an area-interaction component in the point process model of tree recruitment in order to investigate interaction among recruited trees. The outcome of the area-interaction process indicated that trees were recruited in close proximity to other recruits. This aggregation of recruited trees was not caused by non-recruited trees, herbaceous vegetation or wood debris. The fitted radius r of the recruits' neighborhood varied from 31 cm (1A), 37 cm (1B) to 14 cm (2A). Therefore, the radius r decreased with increasing tree density and increasing mean tree crown radius. This indicates that the cluster size of recruited trees is smaller in plot 2A, which was also confirmed by the pair-correlation function.

In these models, a focal tree exerts influence on its neighboring environment within a circular area around its stem. In the Zone-Of-Influence (ZOI) model the radius of this area depends on the tree size, crown area and the extent of its root network belowground (Berger and Hildenbrandt, 2000). According to this concept inter-tree interaction takes place when neighboring trees share the same area (ibid.). However, the fitting algorithm of Gibbs point processes is not capable of fitting a size-dependent interaction radius to each point but assigns the same interaction radius to each point. Thus, the area-interaction component applied here is similar to a Fixed-Radius-Neighborhood (FRN) model (Berger et al., 2008).

The clustering of recruited trees could be a result of short-range seed dispersal originating from other recruited trees (Schurr et al., 2004). Under these harsh environmental conditions, mangrove trees are known to produce propagules already at a very young age (Clarke, 1995). Therefore, it could be possible that trees which were recruited only within the last three years already produced offspring. This offspring established and grew in the seed shadow of its parent tree (McGuinness, 1996). If trees did not produce propagules within this short period of time, they could have facilitated the establishment and further recruitment of propagules transported by tide (Tirado and Pugnaire, 2003). This form of intraspecific facilitation among conspecific *R. mucronata* and *A. marina* seedlings has been described by Huxham et al. (2010) and Kumara et al. (2010).

Regardless of the actual mechanism, the positive interaction among recruited trees and their positive density dependence indicated a positive feedback among recruits which accelerates forest recolonization and development.

2.4.3 HERBACEOUS VEGETATION

Both *S. portulacastrum* and *B. portulacoides* are succulent ground-covering herbaceous plants. In the low-density forest stand, seedling density was higher in

patches of *S. portulacastrum* but not in *B. portulacoides*. The opposite was the case in the high-density forest stand. The sensitivity analysis revealed that seedling establishment might be also influenced by *S. portulacastrum* in plot 2B. However, the available data is not sufficient to provide conclusive evidence.

S. portulacastrum and *B. portulacoides* could have enhanced seedling establishment through the entrapment of floating propagules. Propagule entrapment by herbaceous salt-marsh vegetation has been suggested as an important process which facilitates the colonization of inland salt-marsh areas (Peterson and Bell, 2012) as well as degraded mangrove areas (McKee et al., 2007). McKee et al. (ibid.) conducted field experiments to quantify the propagule retention capacity of salt-marsh plants including the grass *Distichlis spicata* and the succulent *S. portulacastrum* by placing *Rhizophora mangle*, *Avicennia germinans* and *Languncularia racemosa* propagules into herb patches as well as bare areas and comparing their establishment. Both herbaceous plants facilitated the establishment of seedlings of each mangrove species by increasing their retention through trapping. Whereas similar numbers of *R. mangle* propagules were trapped in both herbs, the smaller propagules of *A. germinans* and *L. racemosa* were trapped in higher numbers by the grass *D. spicata* than by *S. portulacastrum*. Peterson and Bell (2012) confirmed these observations through similar experiments and concluded that succulent plants, such as *B. maritima* and *S. portulacastrum*, trap only limited numbers of *A. germinans* propagules. These studies showed that the herb species investigated in my study have a low capacity of trapping *A. germinans* propagules which resulted in a low seedling density.

My analysis also showed that *S. portulacastrum* vegetation cover is significantly positive associated with preceding tree recruitment. Thus, the density of tree recruits in 2014 was higher in herb patches which were mapped in 2011. The sensitivity analysis of the recruitment point process model underlined the importance of herbaceous vegetation on tree recruitment. Extreme negative and positive residual values were associated with bare and herb covered areas respectively which indicates that other underlying factors increase the positive effect of herb cover on tree recruitment in low-density forest stands. One possible explanation is that the herbaceous vegetation cover facilitated upcoming regeneration by ameliorating extreme environmental stress (ibid.).

The outcomes of this study confirm that herbs have a sustained positive effect on mangrove colonization and do not suppress post-dispersal tree development. McKee et al. (2007) found that herbaceous salt-marsh vegetation is not only acting as seed-traps but could also facilitate tree recruitment through amelioration of extreme edaphic conditions, such as temperature and salinity. This has also been shown by Milbrandt and Tinsley (2006) who found that *A.*

germinans seedlings planted in patches of the *B. maritima* were less prone to mortality (69% mortality) compared to seedlings on mudflats (93% mortality).

2.4.4 COARSE WOOD DEBRIS

Including a distance map of coarse wood debris did neither improve the fit of the seedling establishment model nor the fit of the tree recruitment model. This suggests that scattered wood debris did not trap propagules and impact seedling establishment. However, the current model only considered the length of each log. The impact of additional factors, such log diameter, orientation to the main tidal current and its height off the ground on the trapping capacity of wood debris should be investigated further to provide more conclusive evidence about the effect of wood debris on mangrove seedling establishment.

2.4.5 RESEARCH OUTLOOK

The high sensitivity of the seedling process model to herb patches indicated that the results regarding the effect of herbaceous plant cover were inconclusive. This problem can be attributed to the low number of mapped seedlings in low-density forest stands. Therefore, more spatial data of seedlings and herb patches are required in this case. I recommend to increase the plot size in low density forest stands to map at least 100 individuals in one plot.

Shorter time periods between measurements would provide a more fine-scale temporal perspective on forest development. My results showed that forests at this stage can develop at a very fast pace. Seasonal measurements could provide more detailed insights into the relationship between non-recruited trees and tree recruitment in relationship to environmental conditions during dry and rainy seasons.

Lastly, this study lacked environmental data and, thus, the spatial distribution of abiotic covariates, such as salinity, temperature, and photosynthetically active radiation (PAR), could not be considered. In addition, detailed elevation data could provide a better understanding of propagule dispersal processes because even small slopes diverge tidal flow and can hinder propagule dispersal in this flat terrain. I suggest the collection of spatially-explicit environmental data and apply spatial kriging or interpolation techniques (Uria-Diez et al., 2013) in order to include these factors into the point process model of seedling establishment and tree recruitment.

The point process model provided interesting insights into the dispersal behavior of *A. germinans* in high-elevated areas. Di Nitto et al. (2013) developed a

hydrodynamic model to analyze propagule dispersal on a landscape scale in the context of shrimp pond regeneration. The next step in investigating the recolonization of the study site could be to develop a hydrodynamic model in order to understand the relationship between tidal inundation and dispersal patterns after the stand-replacing event.

2.5 CONCLUSION

These results confirm that salt-marsh vegetation acts as the starting point for mangrove recolonization and indicate that the positive interaction among *A. germinans* trees accelerates forest regeneration. This implies that herb vegetation should not be removed in the restoration of degraded mangrove sites but utilized to assist natural regeneration. Aggregation of recruited trees and the positive effect of tree crown cover on seedling density suggests that conspecific trees did not compete or suppress regeneration under harsh environmental conditions. It should be further investigated whether *A. germinans* trees facilitate one another during forest regeneration.

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3 THE IMPACT OF INTRASPECIFIC INTERACTION ON *AVICENNIA GERMINANS* TREES UNDER HARSH ENVIRONMENTAL CONDITIONS

ABSTRACT

The stress gradient hypothesis suggests that plants benefit from facilitative interactions with their neighbors under harsh environmental conditions. However, the effect of interaction among conspecific mangrove trees on focal trees under harsh environmental conditions is unknown. I investigated whether shrub-like *A. germinans* trees in a hypersaline mangrove zone are larger in size when growing in dense clusters or as solitary trees.

Linear regression and spatial point pattern statistics were used to analyze the relationship between the intensity of tree interaction and several tree attributes in three forest plots. Investigated tree attributes included mean internode length, height, basal stem diameter, relative crown displacement and crown area. The interaction intensity or potentially available growing area of a focal tree was quantified with Dirichlet tessellation of each forest plot.

I found that more aggregated *A. germinans* trees were taller and had longer internodes. This positive effect of neighbors on focal trees was stronger in two forest plots of low tree density (1.2 tree m⁻²) than in a denser plot (2.7 trees m⁻²).

Only in this denser forest plot did closely neighboring trees (< 1 m distance) avoid competition through crown displacement but not through increased height growth.

These results indicated a shift from facilitation, i.e. a positive effect of tree interaction, towards a balance between facilitation and competition in denser forest stands. The facilitation among mangrove trees under harsh environmental conditions has important implications for the restoration of degraded mangrove areas. Cluster planting could be used to lower mortality during initial restoration.

3.1 INTRODUCTION

Trees modify their surrounding above- and belowground environment and interact through their influence with neighboring individuals of the same or other species (Fajardo and McIntire, 2011; Pugnaire et al., 1996). Habitat modification by trees includes uptake of resources, such as sunlight, water and nutrients as well as lowering radiation or temperature (Leathwick and Austin, 2001). This habitat modification is often seen only as the uptake of resources and the interaction between neighboring trees is understood as competition for limited resources (Canham et al., 2004). Therefore, solitary trees with more growing space are thought to be able to gain access to more resources and increase their fitness and growth. However, certain habitat modification experienced by neighbors are beneficial for trees. A focal tree modifies its local environment in many ways which either interfere with or facilitate neighboring trees, positive and negative interactions among the same individuals can occur simultaneously (Berkowitz et al., 1995; Callaway and Walker, 1997). The net effect of tree interaction depends on a number of factors, one of them is the level of environmental stress. This shift of balance between competition and facilitation along an abiotic stress gradient has been conceptualized in the stress gradient hypothesis (SGH, Bruno et al. 2003; Maestre et al. 2009).

Facilitative plant interactions have been observed in ecosystems with harsh environmental conditions such as deserts, rocky shores and wetlands (Bertness and Leonard, 1997; Callaway et al., 2000; Choler et al., 2001; Goldberg and Barton, 1992). The stress gradient hypothesis has been developed based on these observations, and assumes that facilitative interactions intensify under abiotic stress. Similarly, elevated mangrove forests are under the greater influence of high salinity and low nutrient availability than lower intertidal areas (Jiménez and Sauter, 1991). Recent studies detected intraspecific facilitation among seedling cohorts in mangrove plantations in elevated areas (Huxham et

al., 2010) and interspecific facilitation between herbaceous plants and naturally recruited seedlings in a degraded mangrove forest (McKee et al., 2007; Milbrandt and Tinsley, 2006).

The interaction among conspecific trees has not been studied yet. Whether mangrove trees facilitate each other under harsh environmental conditions would be of specific interest for the restoration of degraded mangrove areas.

Facilitative plant interactions include a wide range of mechanisms, for instance stress amelioration in harsh environments (Bronstein, 2009). Neighboring plants growing under harsh environmental conditions facilitate each other by ameliorating stress factors and improving their shared habitat (Brooker et al., 2008; Callaway and Walker, 1997). Several studies have reported, that large shrubs provide nurse plant effects by ameliorating environmental stresses and enhancing the establishment, survival, growth and fitness of surrounding smaller and younger plants (Flores and Jurado, 2003; Pugnaire et al., 2011; Pugnaire et al., 1996). The canopy cover of nurse plants provides protection against extreme soil and air temperature and reduces water evaporation compared to the surrounding open area (Padilla and Pugnaire, 2006). Due to these benefits, nurse plant effects appear to be crucial for the survival and growth of vulnerable juvenile plants in arid and semi-arid habitats (Tirado and Pugnaire, 2003).

Trees react to above-ground competition through crown avoidance (Getzin and Wiegand, 2007). Shading by neighboring trees lowers photosynthetically active radiation (PAR) reaching tree crown. Trees adapt to changing light conditions by expanding unshaded branches within the tree crown. Crown plasticity, i.e. the lateral phototropic growth of branches towards high light conditions, is an adaptive mechanism to avoid competition as it requires less energy than increasing height growth (Schröter et al., 2012). Lateral crown expansion results in asymmetric crown. Therefore, a displacement of the crown centroid, its geometric center, from its stem base is a useful indicator of competition because its reactive to the pressure from neighboring trees (Getzin and Wiegand, 2007).

Interspecific facilitation among different plant species has been in the focus of most studies investigating plant facilitation (Brooker et al., 2008). Although similar outcomes can occur among plants of the same species, the number of studies investigating intraspecific facilitation among conspecific plants remains limited (except Eränen and Kozlov, 2008; Fajardo and McIntire, 2011; Franks, 2003). Additional knowledge about intraspecific facilitation might help to improve current restoration approaches currently used in degraded species-poor ecosystems (Wu and Yang, 2013).

This study has been conducted in an elevated mangrove area which is recovering slowly from an extreme forest die-back in order to test whether mangrove

ecosystems follow the stress gradient hypothesis. The main limiting factors for tree growth in this environment are drought, in combination with hypersalinity ($> 100 \text{ ‰}$ at 50 cm sediment depth, Vogt et al. 2014) and intense irradiance. In these elevated areas, the stress-tolerant *A. germinans* reaches the limits of its physiological abilities. The photosynthetic capacity is impaired by osmotic limitations caused by hypersalinity and toxic risks. Although *A. germinans* is a light-demanding tree species (Rabinowitz, 1978b) less sunlight might not limit tree growth. Under intense sunlight radiation photosynthetic capacity may also be reduced due to photoinhibition, i.e. a decline in photosynthetic efficiency caused by excessive sunlight radiation (Osmond, 1994; Sobrado, 1999). Besides causing photoinhibition, high irradiance further reduces soil moisture content and increases leaf evapotranspiration.

In this study, I investigate how competitive and facilitative intraspecific interaction among *A. germinans* is associated with tree growth under different levels of tree density. According to the SGH, trees with more neighboring trees benefit from facilitative interactions under harsh environmental conditions, such as high salinity, low water availability and high solar radiation. If interaction among neighboring trees would result in competition for limited water resources, one would expect trees with more growing space available to have more access to water and in turn grow faster and taller than trees in denser areas. However, more growing space does not necessarily increase access to water as exposed ground which is not shaded by the canopy is prone to drought and evaporation and can provide less soil moisture for trees (Figure 3.1).

I developed three alternative hypotheses. The null hypothesis was that the growth of a focal tree is independent of its growing space. This would imply, that trees do not interact. The first alternative hypothesis was that the growth of a focal tree is negatively related to its growing space due to the facilitative interactions with its neighbors. This would imply, that neighboring trees ameliorate the harsh environmental conditions and improve their neighbors' growth. The second alternative hypothesis was that the growth of a focal tree is positively related to its growing space due to the competitive interactions with its neighbors. This would imply, that *A. germinans* trees are not able to ameliorate harsh environmental conditions and compete with their neighbors for limited resources. In order to test this hypothesis, I used multiple linear regression in combination with spatial pattern analysis in order to cross-validate the findings.

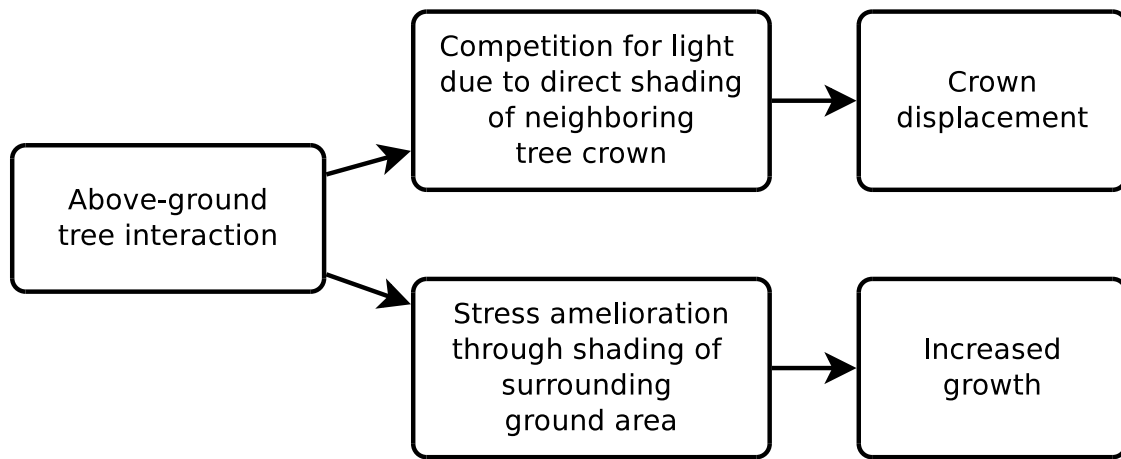


Figure 3.1: Conceptual framework of intraspecific interaction among shrub-like *A. germinans* trees under harsh environmental conditions.

3.2 DATA ANALYSIS

For a detailed description of data collection procedure see section 1.5 on page 12. In this chapter, I analyzed data from plot 1A, 1B and 2A which were collected in 2014. I was not able to conduct a statistical analysis of tree growth or survival due to the small number of trees in 2011.

Crown displacement is frequently used as an indicator of crown asymmetry and plasticity (Longuetaud et al., 2008). The crown projection of each tree's horizontal tree crown extent was constructed based on the measurements of the maximum crown extent in eight cardinal directions. This enabled me to calculate absolute crown displacement, i.e. the distance between the tree stem location and the centroid of the crown projection (Figure 3.2, Brisson, 2001). I calculated crown displacement in order to analyze the influence of inter-tree interaction on crown asymmetry. Specifically, I used the relative crown displacement instead of absolute crown displacement in order to avoid correlation between the independent variables crown area and crown displacement in the linear regression analysis, i.e. collinearity. The relative crown displacement is the ratio of the distance between tree stem and crown centroid and the tree's mean crown radius (Longuetaud et al., 2008). A relative crown displacement value of around 0 indicates that the crown is centered on the tree stem, whereas larger values indicate crown asymmetry. For instance, a relative crown displacement value of 1 implies that the crown shift is equivalent to the tree's mean crown radius.

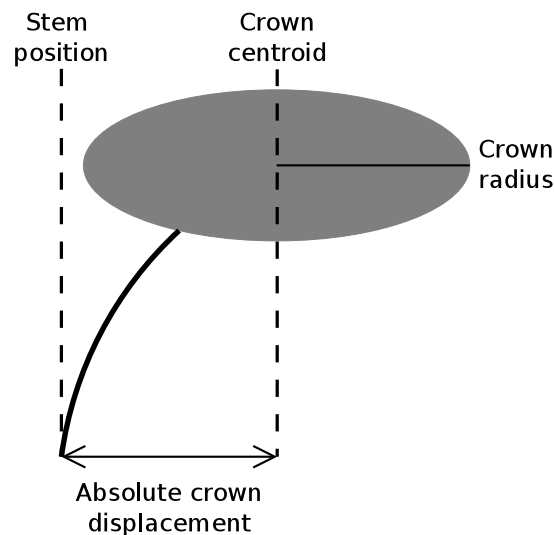


Figure 3.2: The absolute crown displacement of a focal tree is equivalent to the distance between stem position and crown centroid. Relative crown displacement is the ratio of absolute crown displacement of a focal tree and its crown radius.

The influence on interaction among neighboring trees is usually assessed with a wide range of competition indexes which describe in mathematical terms the status of a focal tree within a stand by using structural and allometric measures (Pretzsch, 2009, p. 292). Although both distance- or non-distance-dependent measures of forest structure are used, tree interaction is considered to be spatially-explicit.

I used the area of growing-space potentially available to each tree as an indicator of interaction magnitude. The potentially available growing space of each tree describes the tree's neighborhood density and was calculated using a Dirichlet tessellation approach (Aakala et al., 2013). Forest plots were partitioned into polygons in such a way that each focal tree was located in a separate polygon which describes its potentially available growing space (Figure 3.3). Thus, the growing-space area is determined by the number and distribution of neighbors but independent of the focal tree's crown area. Trees with more neighbors have a smaller growing area, whereas more isolated trees have a larger growing area. The Dirichlet tessellation was computed using the command *dirichlet* based on the tree point pattern. The area of each tessellation polygon was extracted with *tile.areas*. Dirichlet tessellation areas were calculated with the R package *spatstat* (version 1.40-0) (Baddeley and Turner, 2005).

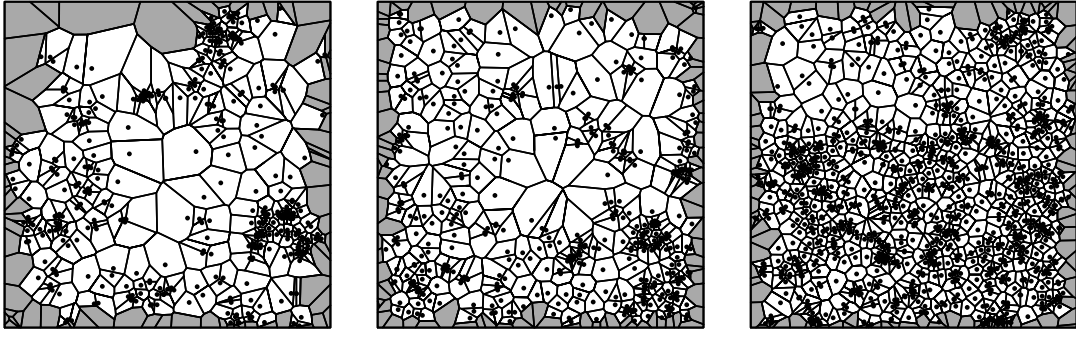


Figure 3.3: Dirichlet tessellation of stem positions of plot 1A (left), 1B (middle) and 2A (right). All focal trees with a tessellation area which shared a boundary with the plot border (grey Dirichlet tiles) were excluded from the regression analysis.

In addition, I used the density-dependent Hegyi competition index CI which was calculated as following

$$CI_f = \sum_{k=1}^n \left(\frac{d_k}{d_f} \right) \left(\frac{1}{r_{fk}} \right), \text{ for } k \neq f \quad (3.1)$$

where CI_f is the Hegyi competition index of focal tree f , d_k is the diameter of a neighboring tree k , d_f is the diameter of focal tree f , r_{fk} is the distance between focal and neighboring tree, and n is the number of neighboring trees for focal tree f (Hegyi, 1974).

Forward stepwise linear regression analyses were conducted in order to analyze how the crown area and growing space of a focal tree (independent variables) are associated with its mean internode length, height, basal stem diameter and relative crown displacement (dependent variables). A null model consisting only of the parameter 'crown area' and a complete model were constructed for each dependent variable and plot in order to analyze the influence of tree size and the additional influence of neighborhood intensity. I chose internode length as an indicator of tree growth. Tree height was used as a second indicator of tree growth because of its sensitivity to the environmental conditions, especially salinity (Peters et al., 2014; Vovides et al., 2014). The tessellation required an edge correction because the potential growing space of focal trees close to the plot border was likely to be overestimated because neighboring trees outside the plot were not considered (Kenkel, 1991). Therefore, all focal trees with a tessellation area which shared a boundary with the plot border were excluded from the regression analysis (Figure 3.3).

Both independent variables, tree crown and growing space, were square-root transformed to meet the assumptions of linear regression, which are the appropriateness of the linear model, the independence, equal variance and normal distribution of errors, and the homogeneity of the sample population (Gelman and Hill, 2006, p. 45). The goodness-of-fit of each regression model was evaluated using its coefficient of determination (adjusted R^2) and the statistical significance (p -value) of each model parameter. In addition, I checked the model assumption regarding the distribution of residuals by inspecting visually residual against fitted values to confirm appropriateness of the linear model and error independence, the Scale-Location plot to confirm the equal variance of errors, the Normal Q-Q plot to confirm the normal distribution of the dependent variables' residuals, and the Residual-Leverage plot to find out whether the sampled population is homogenous (ibid., p. 45).

The differences of tree characteristics and tree neighborhood between three plots were tested with the nonparametric Kruskal-Wallis tests. The nonparametric Spearman rank correlation was used to analyze the correlation among tree characteristics and tree neighborhood.

In addition to linear regression, point pattern analysis was used in order to investigate the relationship of tree interaction and tree size. The recorded forest map of each plot (1A, 1B and 2A in 2014) was simplified to two-dimensional distribution of tree stems and crown centroids. Therefore, the sampled area was represented by the horizontal plane bounded by plot borders, and each tree was represented by a point, defined by coordinates of the tree stem or its crown centroid.

Ripley's K -function $K(r)$ describes the average number of points in a circle of radius r around a focal point over the point density λ of the specified area (Wiegand and Moloney, 2004). It is a cumulative function which considers all points within this circle as the radius r increases. Consequently, spatial patterns at larger scales are confounded with those at smaller scales (Wiegand and Moloney, 2013, p. 47). The pair-correlation function $g(r)$ is based on the K -function but non-cumulative which enables a better assessment of spatial patterns across scales. It is a distance-dependent correlation function based on point-to-point distances and describes the average density of points within a ring of radius r and width dr around a focal point (Wiegand and Moloney, 2004).

$$g(r) = \frac{K'(r)}{2\pi r} \quad (3.2)$$

where $K'(r)$ is the derivative of Ripley's K -function $K(r)$. The value of $g(r)$ indicates how many times the point density at distance r is higher or lower than

the density of a random pattern (Wiegand and Moloney, 2013, p. 49). The univariate pair-correlation function $g(r)$ was used to analyze the distance-correlation of tree stem location as well as crown centroid in order to investigate whether the spatial distribution of crown centroids is more regular than tree stems as a result of crown displacement (Getzin and Wiegand, 2007). The pair-correlation function $g(r)$ can indicate spatial randomness ($g(r) = 1$), clustering ($g(r) > 1$) or regularity ($g(r) < 1$) of trees a distance r apart from each other. Therefore, higher $g(r)$ -values for tree stems than crown centroids at a small distance r would suggest a more regular distribution of tree crown centroids compared to tree stems and consequently show that crown displacement is caused by neighboring trees (ibid.).

In addition to the pair correlation function, which was used to investigate distance-dependence of trees, I applied the mark correlation function $\kappa_{mm}(r)$ in order to analyze the spatial size-correlation of the tree size attributes crown area, basal stem diameter, tree height, mean internode length and relative crown displacement based on the distance r between the stem position of two trees. Thus, the mark correlation function provides information about the dependence of tree attributes at a distance r (Stoyan and Penttinen, 2000, p. 346).

The conditional mean of the product of the quantitative marks of a pair of points, given that they are located distance r apart, are calculated by identifying all point pairs which are separated by distance r and determining the mean size of these pairs:

$$c_{mm}(r) = E_{or}(m(o) \cdot m(r)) \quad (3.3)$$

where $m(o)$ and $m(r)$ are marks of pairs of points at distance r apart (Illian et al., 2008, p. 341).

The nonnormalized conditional mean $c_{mm}(r)$ is normalized with the unconditional mean value over all pairs of points μ^2 :

$$\kappa_{mm}(r) = \frac{c_{mm}(r)}{\mu^2} \quad (3.4)$$

A mark-correlation value $\kappa_{mm}(r)$ higher than 1 indicates that the conditional mean mark value at a certain distance is higher than the mean of all point pairs (ibid., p. 341). Thus, if the mark-correlation $\kappa_{mm}(r) > 1$ tree attributes are on average larger than the population's mean value and thus positively correlated at this distance. If $\kappa_{mm}(r) = 1$, the size of tree attributes is independent at distance r apart and are not spatially correlated. If $\kappa_{mm}(r) < 1$ tree attributes are on average smaller than the population's mean value and negatively correlated at distance r . Therefore, $\kappa_{mm}(r)$ shows whether trees which are separated by

the distance r are of average size smaller or larger than the average tree size.

Corresponding to the mark correlation function, the mark variogram $\gamma_m(r)$ (Penttinen et al., 1992) is based on

$$\gamma_m(r) = \frac{1}{2} E (m_i - m_j)^2 \quad (3.5)$$

which is the squared differences of mark pairs m_i and m_j at distance r apart and normalized by the mark variance, where E is the expectation (Stoyan and Walder, 2000). If $\gamma_m(r) = 1$, the size of tree attributes is independent. If $\gamma_m(r) > 1$ attributes of neighboring trees are different in size which is called negative autocorrelation, whereas if $\gamma_m(r) < 1$ attributes are similar in size, positive autocorrelation (Suzuki et al., 2008). The effects of competitive tree interaction on the spatial patterns of forest has been well-described with mark variograms (Pommerening and Sarkka, 2013). As dominant trees suppress neighboring trees the size dissimilarity between neighboring trees increases and a local size hierarchy establishes (Suzuki et al., 2008). This process results in a negative autocorrelation in the mark variogram, i.e. tree size differentiation (Pommerening and Sarkka, 2013).

I analyzed the effect of interaction on plant growth but not mortality because the latter is caused by much more severe circumstances (Fajardo and McIntire, 2011) and rarely observable. Two measurement periods, three years apart from each other, were insufficient to track all tree deaths.

Local simulation envelopes were calculated in order to test for significant departures of the pair-correlation function from complete spatial randomness at a specific distance r (Wiegand and Moloney, 2013, p. 29). Deviations for mark-correlation function and mark variogram were tested based on independent marking (ibid., p. 35). Hence, envelopes were constructed by fixing the point locations of trees and randomly re-assigning quantitative marks to each point in order to remove spatial associations of marks (Baddeley, 2008). The significance level α of the simulation envelope is given by

$$\alpha = \frac{2k}{m+1} \quad (3.6)$$

where α is the significance level of the simulation envelope, m is the number of simulated random point patterns and k is the rank of the envelope value among the simulated values (Baddeley et al., 2014). Envelopes for all analyses were based on 199 random simulations with the same number of trees as in the

observed forest plots. The boundaries of the Monte Carlo simulation envelopes were formed by the fifth-highest and the fifth-lowest values providing a significance level $\alpha = 0.05$. The R package spatstat (version 1.40-0) was employed for conducting all point pattern analyses (Baddeley and Turner, 2005).

3.3 RESULTS

In total 1712 trees from three forest plots (1A, 1B, 2A) were analyzed. The average density was 1.08 individuals m^{-2} in plot 1A, 1.26 individuals m^{-2} in 1B and 2.70 individuals m^{-2} in plot 2A. The difference in density is also reflected in the significant difference of all tree characteristics. Table 3.1 underlines the dwarfed size of these trees (mean height: 37.1 ± 16.4 cm in plot 1A, 30.1 ± 11.9 cm in plot 1B, 34.2 ± 14.8 cm in plot 2A).

Table 3.1: General characteristics of sampled trees and their growing area in each plot. p -values of Kruskal-Wallis tests are provided.

Variable	Plot	n	Min	Mean	Max	SD
Basal stem diameter (cm)	1A	339	0.4	1.1	4.2	0.5
	1B	409	0.4	1.1	3.5	0.5
	2A	964	0.6	1.3	6.5	0.6
$p < 0.0001$	all	1712	0.4	1.2	6.5	0.6
Tree height (cm)	1A	339	12.0	37.1	100	16.4
	1B	409	8.0	30.1	100	11.9
	2A	964	14.0	34.2	134	14.8
$p < 0.0001$	all	1712	8.0	33.8	134	14.7
Mean internode length (cm)	1A	339	7.1	21.8	51.9	8.9
	1B	409	6.6	18.0	50.7	6.1
	2A	964	4.9	17.9	53.8	6.2
$p < 0.0001$	all	1712	4.9	18.7	53.8	6.9
Relative crown displacement	1A	339	0.0	0.7	2.7	0.5
	1B	409	0.0	0.7	2.7	0.6
	2A	964	0.0	0.5	2.6	0.4
$p < 0.0001$	all	1712	0.0	0.6	2.7	0.5
Tree crown area (dm^2)	1A	339	0.0	7.3	111.8	14.9
	1B	409	0.0	5.9	180.2	14.7
	2A	964	0.0	9.3	275.2	22.5
$p < 0.0001$	all	1712	0.0	8.1	275.2	19.6
Growing area (dm^2)	1A	339	0.8	86.3	830.9	112.7
	1B	409	2.8	81.9	568.2	88.7
	2A	964	0.3	35.5	330.8	32.1
$p < 0.0001$	all	1712	0.3	56.6	830.9	74.5

Crown area and growing space were not correlated, whereas Hegyi-Index and

crown area were significantly positive correlated (Table 3.2). The correlation analysis also revealed that, on the one hand, basal stem diameter and crown area and, on the other hand, tree height and mean internode length were strongly correlated.

Table 3.2: Spearman rank correlation matrix of tree size attributes (Crown area, Mean internode length, Tree height, Basal stem diameter), tree neighborhood measures (Growing area, Hegyi-Index) and Relative crown displacement. All significant correlations are highlighted bold (p -value < 0.01).

	1	2	3	4	5	6
1 Tree crown area	1.00	0.30	0.47	0.78	-0.01	0.56
2 Mean internode length	0.30	1.00	0.62	0.37	-0.12	0.19
3 Tree height	0.47	0.62	1.00	0.57	-0.23	0.43
4 Basal stem diameter	0.78	0.37	0.57	1.00	-0.09	0.72
5 Growing area	-0.01	-0.12	-0.23	-0.09	1.00	-0.42
6 Hegyi-Index	0.56	0.19	0.43	0.72	-0.42	1.00
7 Rel. crown displacement	-0.46	-0.03	-0.17	-0.44	-0.09	-0.28

Regression models were developed for each plot using crown area and growing space area (Dirichlet area) as independent variables and mean internode length (Table 3.3) and tree height (Table 3.4) as dependent variable. The first model included only the variable 'crown area'. In plot 2A a tree's crown area explained internode length (adj. R^2 = 25%) and tree height (adj. R^2 = 49%) much better compared to the same models constructed for the plots 1A and 1B. Crown area was positively related to height and internode length with a similar effect size in all plots.

The second predictor variable, growing space is negatively associated with both dependent variables. In 1A and 1B, tree height and internode length declined much stronger with increasing growing area compared to plot 2A. Only in plot 1A and 1B did the inclusion of focal tree's potentially available growing area increase the adj. R^2 of each model by at least 5-13%, whereas in plot 2A this parameter contributed only marginally (adj. R^2 increased by 0.0% and 1.0%). This shows that the model parameter 'growing area' had a much higher influence on tree size in plot 1A and 1B compared to 2A.

Table 3.5 shows the results of an equivalent regression analysis with basal stem diameter as dependent variable. In contrast to the previous two tree size attributes, the size of potentially available growing space could not explain any variance of the basal stem diameter in both plots.

Corresponding to the previous three regression analyses, a fourth linear regression analysis was conducted to analyze the relationship between relative crown displacement and crown area as well as growing space to investigate if

crown asymmetry was associated with tree interaction, tree size or an unknown factor (Table 3.6). All models have only limited power in explaining crown displacement (Adj. R^2 ranges from 11% to 15%). Despite these limitations, the analysis shows that growing space is not significantly associated with crown displacement in plots 1A and 1B. In contrast, the analysis revealed that focal trees with more neighbors experience more crown displacement in the denser plot 2A. On the other hand, trees in low-density forest stands do not experience pressure from neighbors, whereas trees in denser stands avoid competition.

The Hegyi competition index was positively correlated with crown area and not included in a regression analysis.

Table 3.3: Forward stepwise linear regression analysis of mean internode length and crown area as well as growing space in plots 1A, 1B and 2A. Both predictor variables were square-root transformed.

	Mean internode length					
	Plot 1A		Plot 1B		Plot 2A	
Intercept	18.01*** (0.62)	22.24*** (0.93)	16.31*** (0.40)	19.01*** (0.66)	14.59*** (0.25)	15.39*** (0.47)
Crown area [dm ²]	2.00*** (0.23)	1.93*** (0.22)	0.99*** (0.16)	1.04*** (0.16)	1.49*** (0.08)	1.51*** (0.08)
Growing area [dm ²]		-0.52*** (0.09)		-0.35*** (0.07)		-0.15* (0.07)
Observations	339	339	409	409	964	964
R ²	0.19	0.26	0.08	0.14	0.25	0.25
Adjusted R ²	0.18	0.26	0.08	0.13	0.25	0.25
Residual Std. Error	8.07	7.69	5.82	5.65	5.33	5.32

Note:

*p<0.05; **p<0.01; ***p<0.001

Table 3.4: Forward stepwise linear regression analysis of tree height and crown area as well as growing space in plots 1A, 1B and 2A. Both predictor variables were square-root transformed.

	Tree height					
	Plot 1A		Plot 1B		Plot 2A	
Intercept	28.24*** (1.05)	38.13*** (1.50)	23.12*** (0.65)	30.26*** (1.01)	22.89*** (0.50)	26.12*** (0.92)
Crown area [dm ²]	4.63*** (0.39)	4.47*** (0.35)	4.15*** (0.27)	4.28*** (0.25)	5.03*** (0.16)	5.09*** (0.16)
Growing area [dm ²]		-1.21*** (0.14)		-0.91*** (0.10)		-0.61*** (0.15)
Observations	339	339	409	409	964	964
R ²	0.30	0.42	0.37	0.47	0.49	0.50
Adjusted R ²	0.29	0.42	0.37	0.47	0.49	0.50
Residual Std. Error	13.77	12.50	9.49	8.72	10.53	10.44

Note:

*p<0.05; **p<0.01; ***p<0.001

Table 3.5: Forward stepwise linear regression analysis of basal stem diameter and crown area as well as growing space in plots 1A, 1B and 2A. Both predictor variables were square-root transformed.

	Basal stem diameter					
	Plot 1A		Plot 1B		Plot 2A	
Intercept	0.71*** (0.03)	0.78*** (0.04)	0.71*** (0.02)	0.74*** (0.03)	0.72*** (0.01)	0.68*** (0.02)
Crown area [dm ²]	0.23*** (0.01)	0.22*** (0.01)	0.23*** (0.01)	0.23*** (0.01)	0.26*** (0.004)	0.26*** (0.004)
Growing area [dm ²]		-0.01* (0.004)		-0.004 (0.003)		0.01* (0.004)
Observations	339	339	409	409	964	964
R ²	0.63	0.64	0.73	0.73	0.80	0.80
Adjusted R ²	0.63	0.63	0.73	0.73	0.80	0.80
Residual Std. Error	0.33	0.33	0.24	0.24	0.27	0.27

Note: *p<0.05; **p<0.01; ***p<0.001

Table 3.6: Forward stepwise linear regression analysis of relative crown displacement and crown area as well as growing space in plots 1A, 1B and 2A. Both predictor variables were square-root transformed.

	Relative crown displacement					
	Plot 1A		Plot 1B		Plot 2A	
Intercept	0.88*** (0.04)	0.93*** (0.06)	0.87*** (0.03)	0.83*** (0.06)	0.66*** (0.02)	0.80*** (0.03)
Crown area [dm ²]	-0.10*** (0.01)	-0.10*** (0.01)	-0.12*** (0.01)	-0.12*** (0.01)	-0.06*** (0.01)	-0.06*** (0.01)
Growing area [dm ²]		-0.01 (0.01)		0.01 (0.01)		-0.03*** (0.01)
Observations	339	339	409	409	964	964
R ²	0.13	0.14	0.15	0.15	0.11	0.13
Adjusted R ²	0.13	0.13	0.15	0.15	0.11	0.13
Residual Std. Error	0.51	0.51	0.51	0.51	0.38	0.38

Note: *p<0.05; **p<0.01; ***p<0.001

The pair-correlation function revealed, that in all plots tree stem positions as well as crown centroids are consistently clustered (Figure 3.4). For distances between 20 and 40 cm, $g(r)$ values exceeded the upper limit of the 95% simulation envelopes most strongly. Tree stems are more strongly clustered in plot 1A, whereas plot 1B and 2A have relatively similar and less clustered distribution patterns. The spatial pattern of crown centroids did not differ from the distribution of tree stems in plot 1A and 1B. In contrast, in plot 2A the crown centroids of trees, which were located at a distance of less than 40 cm, were more regularly distributed than their stems. This means that trees in plot 2A avoided competition with neighboring trees through crown displacement.

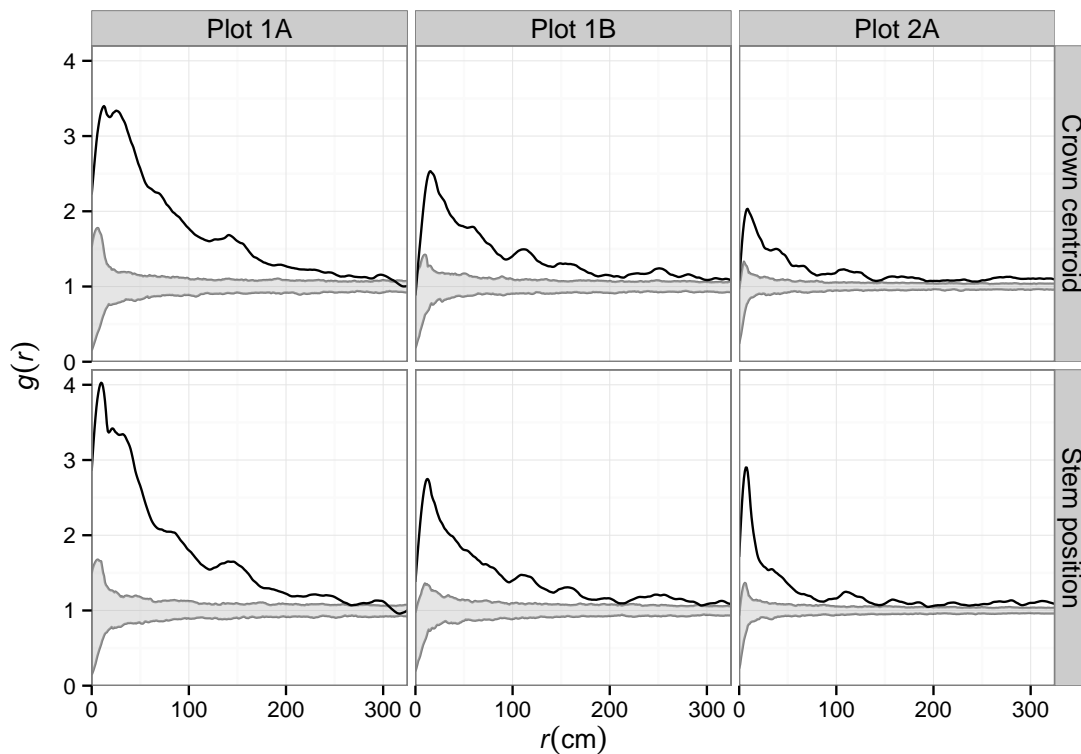


Figure 3.4: The univariate pair correlation function $g(r)$ applied to tree stem position and crown centroid. The grey-shaded area indicates complete spatial randomness (CSR) among points. Values above the simulation envelope indicate clustering, whereas values below would indicate regularity.

I applied the mark-correlation function $\kappa_{mm}(r)$ (Figure 3.5) and mark variogram $\gamma_m(r)$ (Figure 3.6) to five tree attributes, which are crown area, basal stem diameter, tree height, mean internode length and relative crown displacement, based on the stem position of each tree.

The mark-correlation function revealed that tree attributes 'crown area' and 'basal stem diameter' were positively correlated in plot 1A, independent in plot

1B and negatively correlated in plot 2A ($r < 50$ cm). Thus, neighboring trees at a distance of less than 50 cm were larger (1A), similar (1B) and smaller (2A) than the mean size in each plot. On the other hand, both 'tree height' and 'internode length' were positively correlated in plot 1A ($r < 300$ cm) and 1B ($r < 150$ cm), whereas these attributes showed independence in plot 2A. Relative crown displacement was largely distance-uncorrelated in plot 1A and 1B. In plot 2A, crown displacement was strongly positively correlated up to a distance of 120 cm. This means, that closer trees in plot 2A experienced more crown displacement than the mean value.

The mark variograms underlined these differences in the mark processes between 2A and 1A as well as 1B. In plot 2A, all tree attributes showed consistent positive autocorrelation reaching a scale of 25 to 50 cm. Thus, trees pairs which were closer in proximity are more similar in size than those further apart. This is not the case for the magnitude of relative crown displacement which is independent from the displacement of neighbors. Most variograms of plot 1A and 1B show mark independence and there were no negatively autocorrelated mark variogram. In plot 1A, trees show similar tree height and internode lengths up to a distance of less than 50 cm. In plot 1B, only the basal stem diameter is clearly positively autocorrelated.

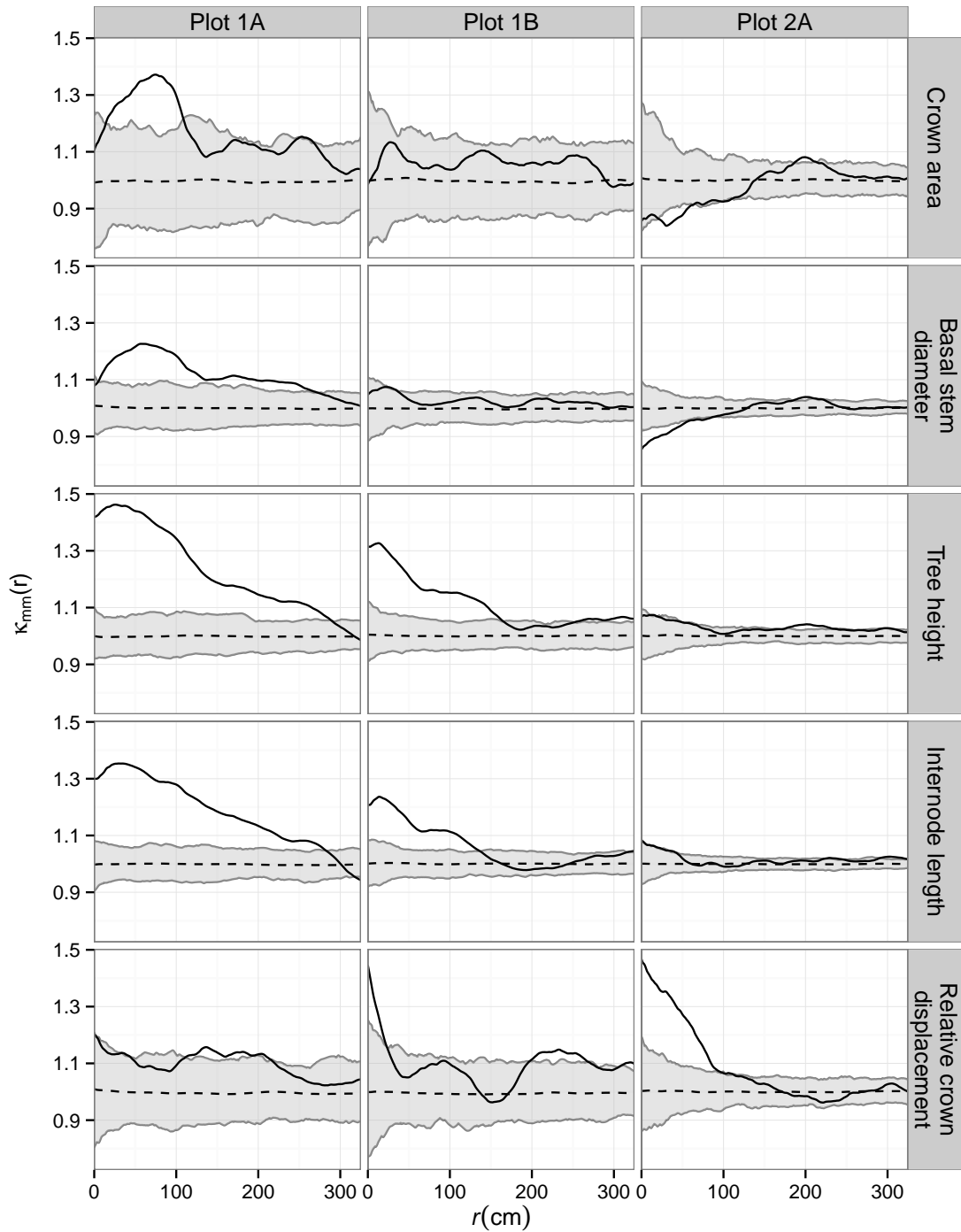


Figure 3.5: The mark-correlation function $\kappa_{mm}(r)$ for tree crown area, basal stem diameter, tree height, mean internode length and relative crown displacement based on stem position. The grey-shaded area indicates mark independence and is bordered by upper and lower simulation envelopes. Values $\kappa_{mm}(r)$ above the simulation band at distance r indicate positive mark-correlation (tree attributes of neighboring trees are higher than the mean value), whereas values below indicate significant negative correlation (tree attributes of neighboring trees are lower than the mean value).

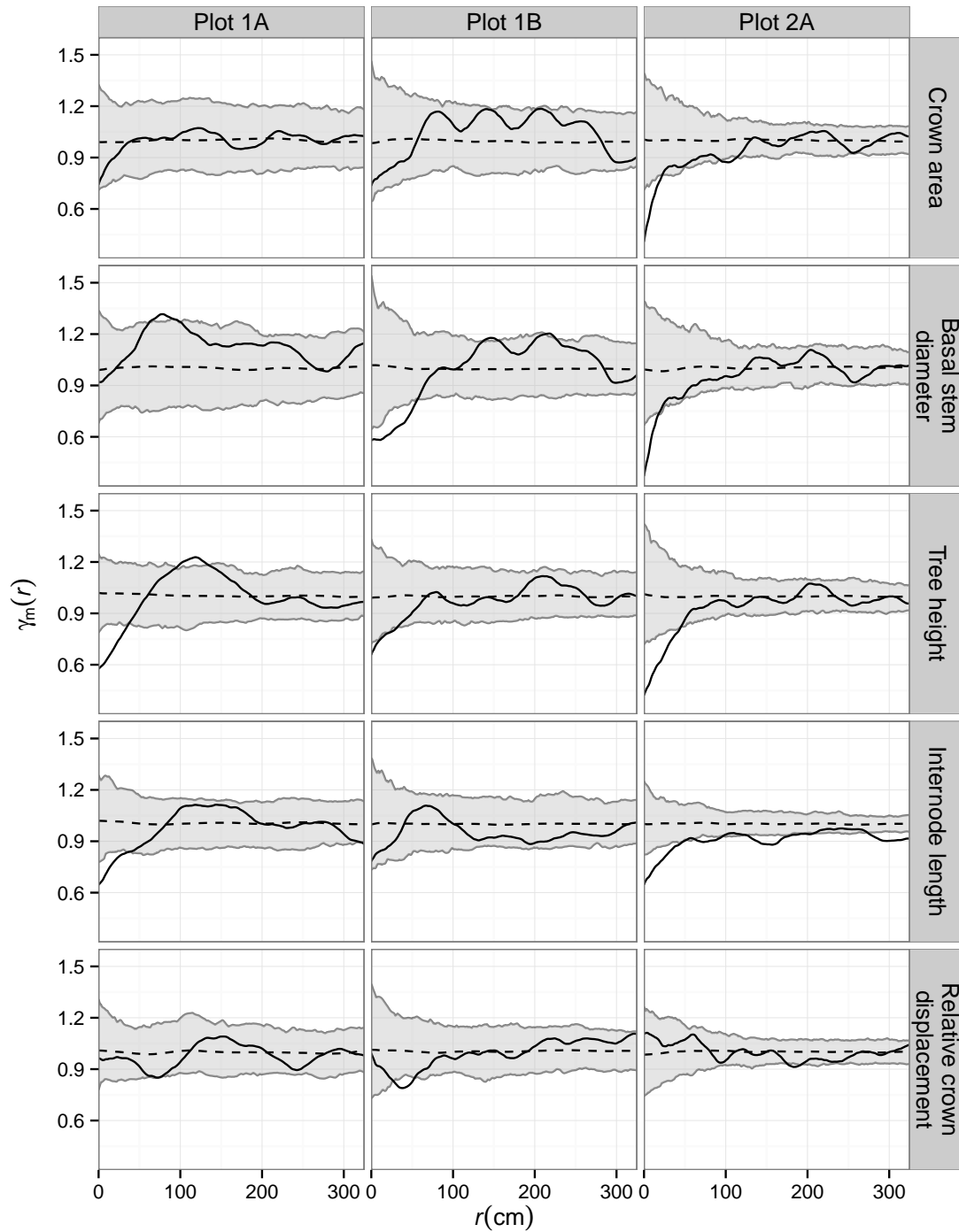


Figure 3.6: The mark variogram $\gamma_m(r)$ for tree size attributes and relative crown displacement based on the tree stem position. All variograms were normalized with the mark variance to 1. The grey-shaded area indicates an independent mark distribution and is bordered by upper and lower simulation envelopes, values above the simulation band indicate significant mark dissimilarity, whereas values below indicate significant mark similarity at distance r .

3.4 DISCUSSION

The spatial pattern analysis revealed a strong aggregation of *A. germinans* trees in the study site. However, the objective of this study was not identify the cause of the observed tree aggregation, but to investigate how intraspecific interaction among strongly aggregated *A. germinans* trees affects their growth in rarely inundated areas. The stress gradient hypothesis suggests that plants benefit from the facilitative effects of their neighbors under harsh environmental conditions, in terms of growth, vitality and survival (Bruno et al., 2003; Callaway and Walker, 1997).

The relationship between the crown area and growing space of a focal tree and its mean internode length, height, basal stem diameter as well as relative crown displacement were analyzed using linear regression analysis. The potentially available growing space of tree was calculated based on a Dirichlet tessellation of each forest plot.

In addition to linear regression, the spatially-explicit mark-correlation function and mark variogram were used to analyze the response of tree characteristics, such as growth, tree size as well as crown displacement, to interaction. I analyzed each mapped forest plot as marked point pattern because both negative and positive tree interactions affect the structure and size distribution of forest stands (Getzin et al., 2008b).

The results of the multiple regression analyses indicated that the growing area of a tree was negatively related to its height and internode length. However, the results of the mark-correlation function showed that tree height and diameter were positively correlated in low density forest stands (1.2 tree m^{-2}) whereas these attributes were negatively correlated in denser stands (2.7 trees m^{-2}). These results are evidence for a shift from facilitation towards stronger competition among trees with increasing tree density.

The pair-correlation function showed that trees in all plots were strongly aggregated. This aggregation was most likely the result of short-range seed dispersal but it could have been also intensified by facilitative interaction among trees. If the likelihood of survival would depend on a larger tree acting as nurse plant then trees would only survive in close distance to each other while isolated trees would die (Brooker et al., 2008). Different ecological processes can cause clustered or aggregated plant patterns which are indistinguishable with point pattern statistics.

Moreover, mortality rates between the two measurement periods, 2011 and 2014, were negligible. The sample size of dead trees was insufficient to conclude how neighborhood interaction affects survival.

3.4.1 THE INFLUENCE OF TREE INTERACTION ON TREE SIZE

The regression analysis revealed that all tree attributes, i.e. basal stem diameter, height and mean internode length, were more negatively associated with the tree's potentially available growing space in low-density plots (1A and 1B) than in high-density stand (2A). Therefore, these measures of tree size increased with smaller available growing space and higher local neighborhood density in less dense stands. In addition, the analysis of the spatial distribution of tree height and mean internode length in plot 1A and 1B with the mark-correlation function underlined that trees in close proximity were taller than more isolated trees. In plot 2A, the height of a tree was independent from its distance to neighboring trees. A density-dependent reduction of tree size caused by competition would result in a negative mark correlation (Getzin et al., 2008b; Getzin et al., 2011). In both stands, tree height was influenced most strongly by the density of neighboring trees, whereas the basal stem diameter was almost insensitive to tree interaction.

Under more benign environmental conditions, the negative relation of tree height and growing space would be evidence of direct shading by neighboring trees because trees accelerate height growth in order to gain access to sunlight above the canopy and to avoid competition for limited sunlight. However, most shrub-like trees in the studied dwarf mangrove forest do not experience direct shading from their neighbors due to the low canopy cover and height limitation caused by hypersalinity. Due to the high salinity levels in the study area, trees are stunted because height growth is extremely impaired.

If competition would be the underlying force of the neighborhood-height relationship, the effect of more growing space on tree height would be positive and stronger in high-density plots compared to less dense stands where the negative pressure from neighbors would be less intensive. However, the results showed a more negative effect of growing space in low-density stands, whereas neighboring trees had a smaller effect on the height of focal trees in high-density stands. Therefore, increased height growth cannot be attributed to increased competitive pressure from neighbors but to the facilitative influences of neighboring trees which enhanced height growth in low-density stands.

Mark variograms exhibited either size independence or a positive autocorrelation of tree size but did not show any negative autocorrelation. Thus, the spatial distribution of tree size was either independent from the location of the tree stem or trees of similar size were aggregated. Positive autocorrelation or tree size similarity is usually found in even-aged forests (Pommerening and Särkkä, 2013). The strong positive autocorrelation of tree heights could be a result of

either the similar age of the mapped trees or the harsh environmental conditions which limit trees to a certain height. Additionally, the mark variograms did not indicate any competition among trees, which usually results in negative autocorrelation (Suzuki et al., 2008).

The positive relationship between neighborhood density and tree size shows that trees do not compete. Otherwise this relationship would be negative. This indicates that the environmental conditions are more benign in tree clusters. However, there are two possible explanation for these findings. The first possible explanation is that the initial site condition within the degraded area was homogeneous. Herbs randomly colonized small areas and trapped propagules. Due to propagule trapping seedlings germinate in clusters. The developing tree clusters improve the surrounding environmental conditions and facilitate each other. The second possible explanation is that the initial conditions inside the plot were not homogeneous. Areas with better conditions were colonized by herbs, whereas less benign areas remained bare. Mangrove propagules were trapped in herbs patches. However, the developing tree clusters did not improve the environmental conditions. Therefore, I cannot conclude with certainty if trees facilitate one another by improving the environmental conditions. Even if I would have measured the environmental conditions during my field study, I would not be able to find out what caused the heterogeneity of site conditions. We can only find evidence for tree facilitation through a controlled field experiment or a long-term observation of recolonization processes.

In conclusion, interaction among trees had a positive effect on tree growth and size in the low-density forest plots. Although these findings indicate facilitative tree interactions, the overall effect of these interactions on tree size was small. The facilitative effect of neighborhood was insignificant in the high-density forest plot 2A. I suggest that in plot 2A the negative and positive influences of tree interaction on tree growth were balanced. None of these results indicate negative effects of neighboring trees on tree size or growth, i.e. competition.

3.4.2 THE INFLUENCE OF TREE INTERACTION ON CROWN PLASTICITY

The comparison of the spatial pattern of tree stems and crown centroids showed that only in plot 2A crown centroids are less clustered than tree stems. In addition to tree height, I also analyzed the effect of neighborhood density on crown displacement because tree branches are quick in adapting to changing sunlight conditions. Thus, it is a more responsive indicator of competition avoidance than tree height (Getzin et al., 2008b).

A. germinans is a light-demanding tree species and thus very sensitive to reduction of sunlight. The linear regression of relative crown displacement and growing space confirmed that trees in a high-density plot react to a higher density of neighboring trees by avoiding competition through crown displacement, whereas trees in low-density plots experience less pressure from their neighbors. Therefore, shade-avoidance response affects the spatial distribution of crown centroids and the magnitude of crown displacement but not tree height. Although crown displacement affects both horizontal and vertical crown dimension, I only considered the horizontal plane due to impaired height growth in dwarf forest. Furthermore, topography was not considered as having an influence on crown asymmetry due to the flatness of terrain.

Crown displacement should be strictly understood as an indicator of competition avoidance, not an indicator of actual tree competition for limited resources which would have negative effects of interaction on the focal tree. Only the regression analysis of basal stem diameter and neighborhood density in plot 2A indicated a negative effects of tree interaction on the size of the focal tree.

The mark-correlation function indicated that trees in plot 2A avoided the crown shade of their neighbors when the distance between them was less than 1 m. I suggest that tree crowns overlapped when trees were located too close and react in order to reduce overlaps between neighboring tree crowns.

3.4.3 MECHANISMS OF TREE INTERACTION

The mechanisms of tree interaction occurring in the study site were not investigated in this study. Trees can potentially benefit from direct shading which increases water use efficiency, and lowers the danger of photoinhibition and extreme temperatures (Armas et al., 2004). The height distribution of the studied stand was homogeneous and thus indicated that trees were too small to shade their neighbors. Although based on my observations, I propose that facilitative interaction among trees is a result of shading of otherwise exposed ground areas (Pugnaire et al., 2011). Neighboring trees are more likely to increase available soil moisture by reducing evaporation by shading their shared environment and as a result could be able to lower the levels of salinity locally (own observation). This form of indirect shading of a tree's surrounding ground area could improve tree growth and reduce possible crown die-back.

The studied interactions were all intraspecific because *A. germinans* is the only tree species which is able to thrive under these harsh environmental conditions. It is therefore difficult to investigate whether the observed facilitative interaction could also occur among different mangrove tree species or if positive

interactions are species-specific (Franks, 2003).

3.4.4 STRESS GRADIENT OR ADVANCED FOREST DEVELOPMENT?

The overall result of this study is that trees benefit more from neighbors and need to avoid less competition in low-density forest stands (plot 1A and 1B) compared to high-density stands (2A). Based on the stress gradient hypothesis, these findings could be an indication of a shifting balance from facilitative to more competitive interaction along a gradient of environmental stress (Callaway and Walker, 1997). I was not able to measure any indicators of environmental stress, such as salinity or soil moisture. Because I cannot associate each plot to an environmental stress level, I can relate my findings only to the tree density but not stress levels. However, there was only a small difference between tree heights in the studied plots. This similarity in tree height indicates that environmental conditions are not necessarily more benign in the more dense forest stand. Higher tree density was maybe not a result of more benign environmental conditions but of longer forest development and earlier recolonization.

Although data from two measurement three years apart from one another were available, the sample size was too small to conduct a meaningful comparison of the relationship between tree size and available growing space. This analysis could have potentially provided a better understanding for the interaction of trees along a trajectory of forest development.

Based on the results and my observations in the field, I hypothesize that neighbors in low-density stands are able to lower soil evaporation, increase the amount of available soil water and reduce the water stress of their neighbors. As tree density increases, this positive density dependence shifts to a negative density dependence because *A. germinans* trees are not able to compensate the increasing water use by shading larger areas. At this point, limited resources availability would induce self-thinning processes which would cause a decline in tree density.

3.5 CONCLUSION

The positive effect of neighboring *A. germinans* trees on conspecific trees suggests that they facilitate one another under harsh environmental conditions. Specifically, trees with less growing area and more intense interaction were taller. This means that facilitation lessens the limitations to tree height growth

imposed by hypersalinity and low soil moisture. The mechanism of facilitative tree interaction has not been studied although I suggest that indirect shading of ground areas is likely to ameliorate harsh environmental conditions. This should be further investigated in future experimental studies. More information about mechanisms of mangrove tree interaction would also be required to design appropriate planting techniques for the restoration of degraded mangrove areas.

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4 INFERRING INTRASPECIFIC NURSE PLANT EFFECTS AND SEED DISPERSAL IN A REGENERATING *AVICENNIA GERMINANS* FOREST STAND USING POINT PROCESS AND INDIVIDUAL-BASED MODELING

ABSTRACT

Point pattern analysis is a useful tool for revealing the presence of past or current ecological processes which are difficult to detect directly. However, various processes can produce similar or identical spatial patterns. In the case of monospecific plant communities, aggregated plant distributions can be the product of short-range seed dispersal and facilitative interactions, such as nurse-plant effects, or both processes.

I used a point process model based on the Thomas cluster process to disentangle the impact of regeneration and interaction processes on the spatial distribution of seedlings and trees. The individual-based model mesoFON was used to compare the suitability of three commonly used spatial summary statistics, pair-correlation function, mark-correlation function and mark variogram, in detecting tree competition and facilitation under different dispersal modes. Both simulations focused on the processes in a regenerating mangrove forest which

is rarely inundated and consists of shrub-like *A. germinans* trees.

I found that 67% of *A. germinans* propagules were further dispersed by tidal currents in a maximum range of approximately 3 m around their parent trees, whereas 33% established in the seed shadow of their parent trees in the study site. Trees were neither acting as nurse plants nor interfered with seedling establishment. Mark-correlation function was the only spatial summary statistics that detected differences between competitive and facilitative tree interaction.

In general, this study shows how point process modeling can be used to infer multiple ecological processes from observed plant patterns. The clustering of seedlings around trees was caused by short-range seed dispersal and not by nurse-plant effects of trees. In addition, the mark-correlation function is a suitable method for detecting positive and negative tree interaction regardless of dispersal processes and requires only information about static tree size not dynamic growth data.

4.1 INTRODUCTION

Spatial pattern analysis is not only useful for describing the spatial distribution of plant communities but can also be utilized to infer underlying ecological processes from observed spatial patterns (Barot et al., 1999; Schurr et al., 2004). As plant communities are structured by a multitude of present and past processes, each process creates a signature in the spatial arrangements of individual plant. The application of spatial pattern analysis is especially useful in forest ecology where processes operate over long time periods and are difficult to monitor (Gray and He, 2009). Nevertheless, the inference of underlying processes from observed tree distributions remains a major challenge for spatial ecologists .

Establishing a causal relationship between a particular process and an observed spatial pattern can be constrained by the fact that various processes can produce similar or identical spatial patterns (McIntire and Fajardo, 2009; Perry et al., 2006; Velázquez et al., 2014). The emergence of aggregated spatial patterns of the same tree species can be the result of three different processes: (1) short-range seed dispersal (Seidler and Plotkin, 2006), (2) environmental heterogeneity (Getzin et al., 2008a) or (3) facilitative tree interaction (Schleicher et al., 2011). Regular tree distributions develop when competition restricts the development of upcoming regeneration to forest gaps or self-thinning results in the death of suppressed trees (Kenkel, 1988). A growing number of studies seek to investigate and disentangle these multiple ecological processes through the use of point pattern analysis (Schleicher et al., 2011). However, the identifica-

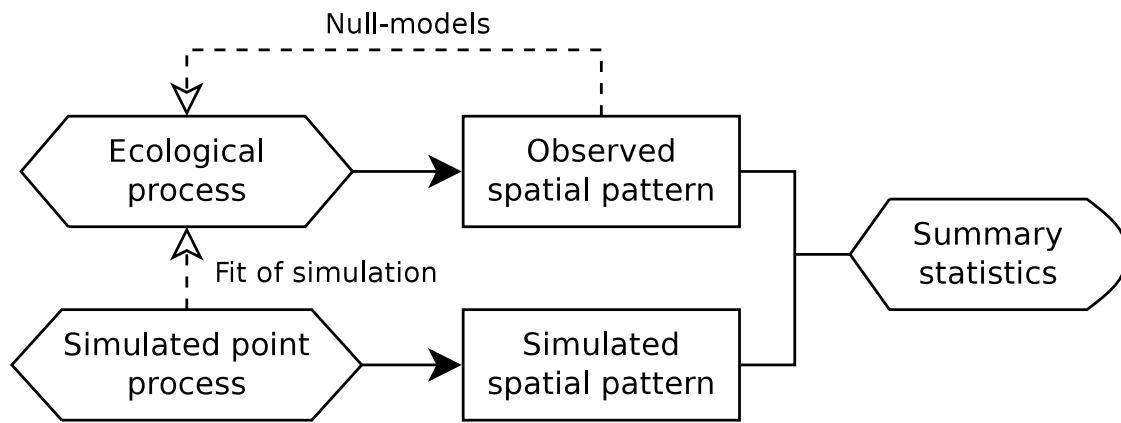


Figure 4.1: Analytical framework for spatial point modeling.

tion of specific spatial processes through point pattern statistics has not been undertaken in monospecific plant communities consisting of only one species.

Inference based on spatial point pattern analysis requires appropriate null models, i.e. hypotheses which link each ecological process to a clearly identifiable spatial point pattern (McIntire and Fajardo, 2009; Wiegand and Moloney, 2004). The most frequently used null model is complete spatial randomness (CSR) which shows whether a point pattern exhibits clustering or regularity. However, CSR is generally not the most appropriate null model in ecological investigations. Other more appropriate null models are based on survival and growth data collected in time-series, e.g. investigating the random mortality hypothesis requires information about the survival and mortality of plant individuals in a community (Kenkel, 1988). Although spatio-temporal data sets can provide valuable insights into the dynamics of plant communities (Raventós et al., 2010), long-term monitoring of early-successional forest ecosystems is uncommon and information about early forest dynamics are rarely available. In addition, the majority of tropical tree species, including mangroves, do not create annual growth rings and, as a result, the age of tropical trees cannot be easily back-dated (Menezes et al., 2003). In conclusion, more complex null models than CSR are required to investigate many ecological processes but the required spatio-temporal data of plant growth and survival are not available.

Complex point process models can act as substitutes for null models based on spatio-temporal data (Law et al., 2009). Simulations with point process models as well as individual-based models can be used to distinguish the effect and relative importance of underlying processes. Simulations are used to recreate the observed point pattern by using point processes analogous to ecological processes. Spatial summary statistics are then applied to confirm the simulation's appropriateness by comparing simulated and observed point patterns (Figure 4.1).

In contrast to terrestrial early-successional forests (Swanson et al., 2011) developing mangrove forests are dominated by one tree species. After a stand-replacing event environmental conditions change drastically due to exposure to sunlight, higher soil temperatures, lower levels of soil moisture and lower nutrient levels. The forest structure of developing mangrove forests is characterized by a high density of small-sized trees, which are often dwarfed due to extreme environmental conditions, and spatial heterogeneity due to the alteration of exposed forest gaps and closed forest canopy. Contrary to mature forest stands, it is difficult in early-successional forests to separate distinct life-stages apart from seedlings and trees. Usually trees are either too young or too slow-growing to be classified according to common life-stage classification systems. Tree mortality is also difficult to observe posterior because decaying remains are less visible compared to old-growth forests where tree stumps remain for many years.

This study investigates the application of two different simulation approaches, point process modeling and individual-based modeling, in two parts. The objective of the first part was to distinguish two intraspecific processes shaping the spatial distribution of *Avicennia germinans* seedlings and shrub-like trees in early forest development under harsh environmental conditions, seed dispersal and tree-seedling interaction, using point process modeling. The objective of the second part was to test whether commonly used summary statistics for unmarked and marked point patterns are appropriate for the analysis of different levels of tree interaction on tree growth under the influence of limited seed dispersal.

The dispersal of mangrove propagules and the resulting spatial distribution of seedling establishment is governed by tidal currents (Clarke et al., 2001). Mangrove areas at high intertidal elevation are inundated infrequently and water levels remain low. Furthermore, *A. germinans* is characterized by a relatively long fruit-fall period of 5 months and dispersed propagules experience different tidal conditions (Menezes et al., 2008). Thus, not all propagules may be dispersed further by tidal currents after parting from their parent tree, but establish within the seed shadow (McGuinness, 1996). The probability of tidal dispersal of propagules after their landing depends on whether seeds start to root before the next tidal inundation. In conclusion, the post-dispersal distribution of hydrochorous propagules is influenced by the frequency of inundations and the strength of tidal currents.

Propagules immediately root after their landing and are not buried as seed bank (Balke et al., 2011). Following their dispersal newly emerging seedlings are immediately interacting with neighboring trees. The spatial arrangement of emerging seedlings relative to their parent trees or other neighboring trees de-

termines the intensity of interaction. Less seedlings would be found in close proximity to trees if trees would interfere with the development of propagules after their settlement, for example by obstructing sunlight. On the other hand, a positive spatial association of seedling around trees would be the result of a facilitative effect of trees on seedling establishment (Felinks and Wiegand, 2008). Beneficial nurse-plant effects of larger plants on surrounding regeneration has been observed in many ecosystems which are under the influence of harsh environmental conditions typical for recovering forest ecosystems (Flores and Jurado, 2003; Padilla and Pugnaire, 2006; Pugnaire et al., 2011). Nurse plants protect sensitive seedlings by ameliorating harsh conditions, such as extreme temperatures, radiation, water stress, through shade (Gómez-Aparicio et al., 2005b; Gómez-Aparicio et al., 2008). Similar effects of *A. germinans* trees could enhance the establishment of conspecific seedlings under harsh environmental conditions.

In the first part, I utilized point process modeling in order to investigate the seed dispersal and intraspecific interaction of *A. germinans* trees and seedlings. First, I combined multiple point process models to investigate barichorus and hydrochorous seed dispersal processes as well as the effect of trees on seedling establishment. Three point process models were used: (1) Thomas process to model limited seed dispersal, (2) independent random perturbation to simulate tidal seed dispersal, (3) random thinning of seedlings dependent on neighboring trees. Each resulting simulated point pattern was compared with empirical data from a regenerating mangrove forest dominated by *A. germinans* in Pará, Northern Brazil.

In the second part, I compared the appropriateness of spatial summary statistics in detecting different levels of tree interaction in short-range and long-range propagule based on simulated *A. germinans* forests. The intensity and level of interaction among neighboring trees is a major determinant of tree growth, and consequently tree size (Getzin et al., 2006). Unmarked point pattern analyses, such as the pair-correlation function $g(r)$, are only applicable for describing the effect of tree interaction on tree survival or mortality, but not tree growth. Thus, marked point patterns are often used to analyze the relationship between the spatial arrangement of trees and their growth (Schlather et al., 2004; Suzuki et al., 2008). The most frequently used statistical tools to analyze marked point patterns are the mark-correlation function $\kappa_{mm}(r)$ and the mark variogram $\gamma_m(r)$. However, when upcoming regeneration is clustered around parent trees, the effect of interaction on tree size might overlap with short-range dispersal processes. This would make the described methods unsuitable for uncovering whether tree interaction is competitive or facilitative.

In contrast to the first part, I used the individual-based mangrove forest dynamics model mesoFON to study the effect of changing levels of tree interaction and seed dispersal on the spatial distribution of tree size in the second part of this study. mesoFON is a simulation model which has been developed to investigate tree-to-tree interactions among mangrove trees in the Neotropics (Grueters et al., 2014). The effect of tree interaction and environmental conditions on mangrove seed dispersal, tree recruitment, growth and death is simulated to model mangrove forest dynamics (ibid.). In order to study recolonizing *A. germinans* forests, the mesoFON model was parameterized to the growth of *A. germinans* under extreme environmental conditions using field data.

4.2 METHODOLOGY

Three simulation experiments were conducted in this study to understand (1) propagule dispersal, (2) seedling establishment and (3) tree growth of *A. germinans* under harsh environmental conditions (Figure 4.2). The first two simulation are based on point process modeling, the third simulation was carried out with the individual-based mangrove model mesoFON.

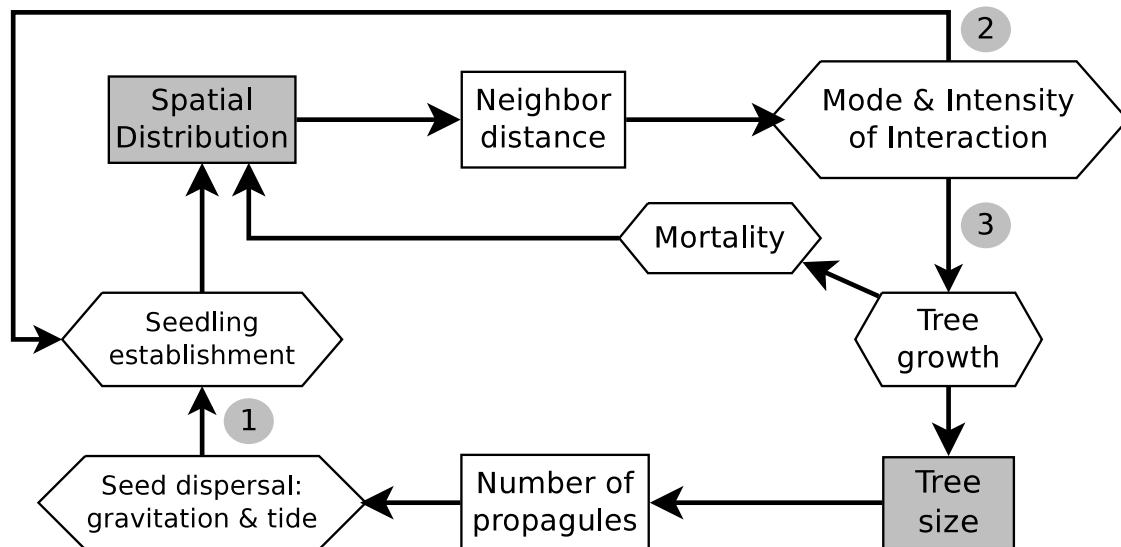


Figure 4.2: Flowchart of ecological processes (hexagon) and measurable properties and patterns (rectangle) driving mangrove forest dynamics. Grey-shaded rectangles represent measurable indicators. Each number corresponds the processes investigated in this study: (1) seed dispersal, (2) impact of tree interaction on seedling establishment and (3) impact of tree interaction on tree growth. Notice how multiple processes affect simultaneously the spatial distribution of stem position and tree size (grey rectangle).

4.2.1 POINT PROCESS MODELING OF SEED DISPERSAL AND SEEDLING ESTABLISHMENT

I fitted a specific type of Poisson cluster process, the Thomas point process model (Thomas, 1949), to the observed seedling distribution data because of its suitability for modeling clustered point patterns (Wiegand et al., 2007). The Thomas process is modeled based on three parameters, the intensity of parent points (κ), the mean number of points in each cluster (μ) and, the standard deviation of a bivariate Gaussian distribution (σ) which specifies the strength of clustering. The model is developed in three steps. First, the locations of parent points with intensity κ are generated by a homogeneous Poisson process or provided by a density map representing observed point intensity. Second, each parent produces a random number of offspring with the mean intensity μ . Third, the distribution of the generated offspring around each parent follows a Gaussian dispersal kernel $N(0, \sigma^2)$. Therefore, the model parameter σ is used to describe the typical size of each cluster in which 68% of all offspring are located away from the parent. The location of offspring is independent of one another and their dispersal direction is isotropic, i.e. direction-independent. I employed the Thomas process due to the similarity of this modeling procedure to natural short-range seed dispersal processes which make each model parameter biologically interpretable (Eichhorn, 2010; Wiegand et al., 2007). A second point processes which generates clustered point patterns is the Matern process (Matern, 1960). This process has not been utilized in this study, because offsprings are randomly distributed within each cluster and reflect rather environmental heterogeneity than limited dispersal processes (Wiegand and Moloney, 2013, p. 318).

Following Seidler and Plotkin (2006) as well as Wiegand et al. (2007), I estimated dispersal parameters of the observed seedling pattern through a Thomas cluster process. For each plot, I simulated gravitational seed dispersal processes in the observed mangrove forest by applying a Thomas cluster process to the observed intensity κ of *A. germinans* trees. Figure 4.3 shows a detailed illustration of the point process model. The standard deviation of the cluster size σ was based on the mean crown radius. I did not consider wind to have a significant effect on seed dispersal as propagules might not have fallen more than 4 cm considering the small height of the parent trees. The range of gravitational dispersal processes are limited to small spatial scales by tree height, crown size and canopy height. Thus, the scale of aggregation of gravitationally seeds is set by physical factors which determine the dispersal distance σ . The average number of offsprings per cluster μ was based on the ratio of the total number

of seedling and trees in each plot.

In order to simulate tidal dispersal processes following seed landing, I applied a random perturbation to randomly selected offspring points which were generated with the Thomas process. I randomly labeled a certain proportion of generated offspring points as 'settled' or 'dispersed' (Baddeley, 2008) because not all propagules are dispersed by tidal currents after their landing. The 'dispersed'-labelled points were subjected to an independent random displacement by distributing each point uniformly in a circle of a radius which corresponds to the maximum tidal dispersal range (*ibid.*). I chose a circular perturbation process instead of a one-directional point pattern shift because floating propagules are, first, transported landwards as well as seawards depending on the tide and, second, locally redirected by obstacles, such as wood debris, herbaceous plants, or small ridges. The tidal seed dispersal model is used to fit two parameters: (1) the probability of tidal dispersal which corresponds to the proportion of labeled offspring points, and (2) the maximum distance of tidal seed displacement which corresponds to the radius of the random point perturbation.

A thinning procedure was applied to the point patterns generated by the seed dispersal models in order to simulate different effects of trees on seedling establishment (*ibid.*). Offspring points were either randomly deleted or retained according to a retention probability ρ which was dependent on the distance to the nearest tree. Each tree exhibits a circular area of influence in which it acts upon seedling establishment. Thus, the thinning procedure of this point process model is similar to a Fixed-Radius-Neighborhood (FRN) model (Berger et al., 2008) because all trees in each plot were assigned the same interaction radius which corresponds to the mean crown radius of each plot. The point retention probability corresponding to the probability of seedling establishment was set to 75% inside and 25% outside the tree's FRN in order to model a facilitative influence of trees on seedling establishment. That means that seeds with nearest neighboring tree closer than the FRN-radius had a probability of 75% to establish, whereas seedlings further away had only a establishment chance of 25%. The values were reversed, 25% inside and 75% outside, to simulate competition. In a third model, offspring points were thinned independent of the distance to the nearest tree with a retention probability of 50% both inside and outside the FRN-radius in order to model point patterns that would arise without the influence of trees on seedling establishment. Retention probabilities of 25% and 75% were chosen to model low and high levels of seedling establishment instead of the establishment of all (100%) and no (0%) seedlings. These values were not chosen to fit the point process to each observed seedling pattern but to observe how the pattern in each plot would change under a similar influence

of trees on seedling establishment following seed dispersal.

By using this complex point process model, I was able to take both dispersal processes and intraspecific interaction into account when analyzing the observed seedling pattern. This point process model only considered small-scale clustering within the plot boundaries which can be attributed to plant interactions and are not generated by environmental heterogeneity which would create large-scale aggregations beyond the scope of each plot (Wiegand et al., 2007).

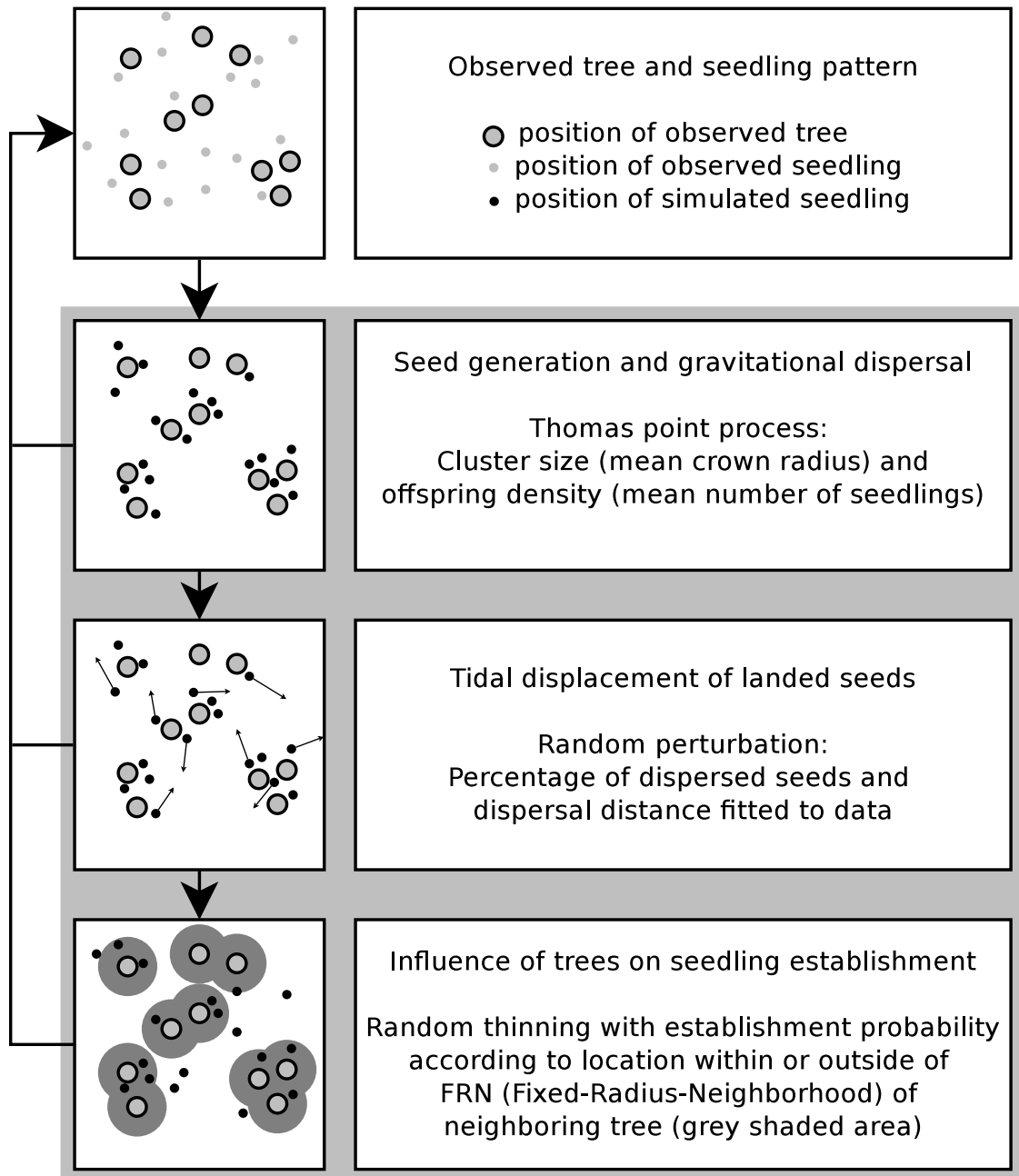


Figure 4.3: Point process model of seed dispersal and seedling establishment. Each ecological process and the corresponding point process are described and illustrated.

The goodness-of-fit of each point process model was also evaluated by com-

paring the observed distribution of seedlings around trees with simulated realizations of the developed point process model based on the bivariate nearest neighbor distance distribution function $G_{seedling-tree}(r)$ and the bivariate pair-correlation function $g_{seedling-tree}(r)$. The bivariate nearest neighbor distance distribution function $G_{seedling-tree}(r)$ shows the probability of a seedling having its nearest neighboring tree at distance r (Illian et al., 2008) and permits the fitting of each dispersal parameter to the maximum distance between seedling and trees. I employed $G_{seedling-tree}(r)$ to fit the radius of random perturbation to the maximum range of tidal seed dispersal and the point labeling probability to the probability of tidal dispersal.

The bivariate pair-correlation function $g_{seedling-tree}(r)$ is a distance-dependent correlation function based on seedling-to-tree distances and describes the density of seedlings at a given radius r from a tree (Wiegand and Moloney, 2004). I used $g_{seedling-tree}(r)$ to analyze the distance-correlation of seedlings and trees at small distances to examine the goodness-of-fit of each interaction model.

The goodness-of-fit of each dispersal parameter was tested by comparing the deviation of the observed seedling distribution from Monte Carlo simulation envelopes which were constructed by repeating each point process simulation 199 times. The boundaries of the 199 simulation envelopes with a significance level $\alpha = 0.05$ formed by the fifth-highest and the fifth-lowest values (Baddeley et al., 2014). Simulation envelopes were generated for the bivariate nearest-neighbor distance distribution function between seedlings and trees $G_{seedling-tree}(r)$ and the bivariate pair-correlation function between seedlings and trees $g_{seedling-tree}(r)$.

Two sensitivity analyses of the seedling establishment model were conducted to investigate how much a variation of the dispersal parameters, dispersal distance and probability, would change the interpretation of the seedling establishment model.

Wiegand and Moloney (2013, p. 15) recommend a minimal sample size of 70 points for point pattern modeling. However, in 2011 there were only 12 and 24 seedlings in plot 1A and 1B, respectively. Thus, I excluded plots 1A (2011) and 1B (2011) from the subsequent analysis. The R package spatstat (version 1.40-0) was employed for conducting all point process models and analysis (Baddeley and Turner, 2005).

4.2.2 INDIVIDUAL-BASED MODEL MESOFON

mesoFON is a individual-based model which has been developed to investigate tree-to-tree interactions among mangrove trees in the Neotropics (Grueters et al., 2014). This model simulates the dynamics of mangrove forests which in-

cludes the effect of tree interaction and environmental conditions on mangrove seed dispersal, tree recruitment, growth and death (ibid.). mesoFON describes each individual tree by its stem position, age, size and annual growth, i.e. diameter, height, crown area, stem volume. In order to simulate the influence a tree exerts on its environment, each tree is surrounded by a scalar above-ground field of neighborhood (FON). The radius of each FON is determined by its basal stem radius (ibid.). Trees interact when both their FON overlap. Three processes are simulated and scheduled in the following order: (1) recruitment, i.e. propagule production and dispersal, (2) tree growth as modified by competition and environment, and (3) natural tree mortality. Although mesoFON has the ability to account for crown plasticity and disturbances but these options were disabled during the experiments (ibid.).

TREE RECRUITMENT

In the simulation experiments two types of propagule dispersal were implemented. Propagules were randomly and uniformly dispersed over the plot to simulate long-range dispersal or propagules were dispersed in a limited range around their parent tree and transported 1 m farther after landing to simulate short-range dispersal.

The number of propagules produced by an individual tree depends on its crown surface area and the model parameter 'propagules per m² crown surface area' which is set prior to the simulation (Table 4.1). mesoFON does not simulate early self-thinning processes among upcoming regeneration because new individuals are insert in as seedlings with a height of approximately 6 cm. Thus, the model parameter 'propagules per m² crown surface area' represents a maximum number of seedlings rather than a maximum number of propagules per crown surface area. For this reason, I did not use the observed number of seedlings per crown surface area but a propagule density which resulted in a tree density which corresponded to the observed tree density.

TREE GROWTH

Tree growth in mesoFON follows a species-specific parameterized Shugart growth function (Shugart, 1984) which simulates the growth of an isolated tree independent of its neighbors and is influenced by its neighbors and the environment (Botkin et al., 1971). This following equation describes the annual diameter increment

$$\frac{\Delta d}{\Delta t} = \left(G \cdot d \cdot \frac{1 - \frac{d \cdot h}{d_{max} \cdot h_{max}}}{3b_2 d - 4b_3 d^2} \right) f_{corr} \quad (4.1)$$

where d is the basal stem diameter at ground level of a focal tree, d_{max} is the maximum attainable basal stem diameter, h is the tree height, and h_{max} is the maximum achievable height (modified from Grueters et al., 2014). The correction factor f_{corr} (equation 4.10) is used to adjust stem volume growth to the positive and negative influence of environment and tree interaction (Botkin et al., 1971). G denotes the initial growth rate of a sapling (cm yr^{-1})

$$G = \frac{\Delta d_{max} \cdot h_{max}}{0.2 \cdot d_{max}} \quad (4.2)$$

b_2 and b_3 denote auxiliary growth parameters which are derived from

$$b_2 = \frac{2(h_{max})}{d_{max}} \quad (4.3)$$

$$b_3 = \frac{(h_{max})}{d_{max}^2} \quad (4.4)$$

The tree height h of a focal tree is derived from the basal stem diameter d based on the following height-diameter relationship (Berger and Hildenbrandt, 2000)

$$h = b_2 d - b_3 d^2 \quad (4.5)$$

In contrast to Grueters et al. (2014), the constant sapling height of 137 cm (breast height) was excluded from the height-diameter equation 4.5 as well as from the diameter growth equation 4.1 in order to adjust the calculations to the basal stem diameter at ground level.

TREE INTERACTION

Each tree influences its above-ground environment and hence neighboring trees within the range of its circular field-of-neighborhood (FON). The intensity of interaction $FON(r)$ exerted by a tree at radius r follows

$$FON(r) = \left\{ \begin{array}{ll} \text{for } 0 < r \leq bsr \rightarrow I_{max} - I_{reduction} \\ \text{for } bsr < r \leq R_{FON} \rightarrow \frac{I_{max} - I_{reduction}}{e^{c \cdot bsr}} e^{c \cdot r}, \quad c = \frac{\ln(I_{min})}{R_{FON} - bsr} \\ \text{for } r > R_{FON} \rightarrow 0 \end{array} \right\} \quad (4.6)$$

where bsr is the basal stem radius at ground level (m), R_{FON} is the radius of

the FON (m), I_{max} is the maximum intensity of interaction inside the tree stem, I_{min} is the minimum intensity of interaction at R_{FON} , defined as a fraction of I_{max} . However, this FON was transformed to a zone-of-influence (ZOI) with a homogeneous intensity I_{max} of 0.3 by setting I_{min} to 0.999 (Figure 4.4). Different levels of tree interaction were simulated by changing $I_{reduction}$. A FON with values of $I_{max} - I_{reduction} > 0$ for the above-ground FON would negatively affect the growth of neighboring trees (competition), whereas a value below 0 would increase their growth (facilitation).

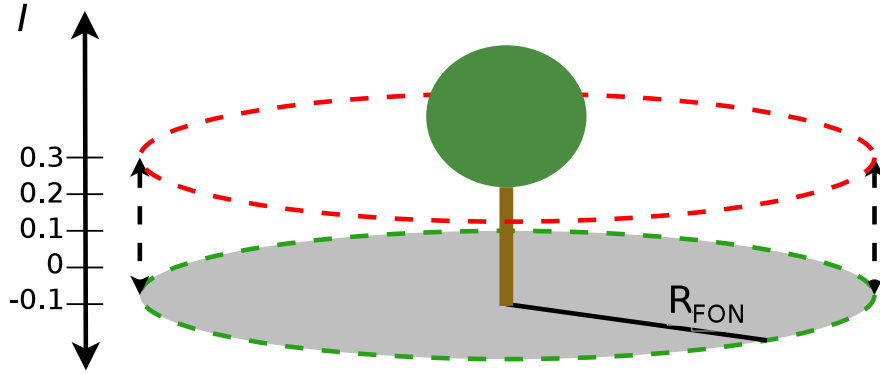


Figure 4.4: The flat field-of-neighborhood (FON) of a tree describes the intensity of interaction I . Different values of I were used to simulate positive and negative above-ground interaction among trees.

The radius of the FON R_{FON} is given by the allometric relationship

$$R_{FON} = a \cdot bsr^b \quad (4.7)$$

where bsr is the basal stem radius (m) of the tree, a and b are allometric scaling parameters (Fontalvo-Herazo et al., 2011).

The interaction intensity at location x, y is calculated by adding the intensity of all overlapping $FON(x, y)$ by

$$FON(x, y) = \sum_n FON_n(x, y) \quad (4.8)$$

Neighboring trees interact when their FON overlap. The total influence F_A^k acting upon a focal tree k as a result of interaction with n neighboring trees is derived by adding the integrals of all FON overlaps

$$F_A^k = \sum_{n \neq k} F_{A_k}^n = \sum_{n \neq k} \int_{A_k} FON_n(x, y) da \cdot asym(d_k - d_n), \text{ if } d_k < d_n \quad (4.9)$$

where the asymmetry coefficient $asym$ controls the interaction intensity act-

ing upon the focal tree depending on the difference between the focal tree's diameter d_k and the neighboring tree's diameter d_n . This asymmetric effect of tree size was applied to simulate a nurse plant effect of larger on smaller trees.

Environmental factors were uniformly distributed and affected all trees in the same manner. In this simulation study only tree interaction was considered to impact tree growth by

$$f_{corr} = 1 - 2F_A^k \quad (4.10)$$

Positive interaction values would reduce the growth of neighbors (competition), whereas negative values would increase their growth (facilitation).

TREE DEATH

Tree death occurs in the model when a tree stops to grown in diameter for five years.

SIMULATION EXPERIMENTS

In order to study recolonizing *A. germinans* forests, the mesoFON model was parameterized to the *A. germinans* growing under extreme environmental conditions using field data from plot 2A in 2011 and 2014 (see Appendix on page 139). Previous studies using mesoFON or its predecessor KIWI investigated the stand dynamics of mangrove forests under benign site conditions. Thus, I was not able to compare this parameterization of a dwarf forest influenced by harsh conditions to similar models.

I conducted simulation experiments with two different modes of seed dispersal, long-range seed dispersal and short-range seed dispersal, in combination with five different levels of tree interaction ranging from competitive ($I_{max} - I_{reduction} > 0$) to facilitative interaction ($I_{max} - I_{reduction} < 0$) by changing the minimal intensity of tree interaction I_{min} . Each model was repeated 20 times. In total, 200 simulation runs were conducted, each model run was stopped after 16 time steps which is equivalent to 17 years. For this simulation experiment was parameterized to a regenerating *A. germinans* forest stand in order to study dynamics of early forest development. Therefore, the simulation was ended after reaching a tree density of more than 10 individuals m^{-2} . All simulation parameters are summarized in Table 4.1.

I applied the mark correlation function $\kappa_{mm}(r)$ in order to analyze the spatial size-correlation of the tree size based on the distance r between stem position of two trees. Thus, the mark correlation provides information about the depen-

Table 4.1: Settings for mesoFON simulation experiments

Parameter	Description	Value
a	Allometric scaling factor of FON	10.637
b	Allometric scaling factor of FON	0.755
Δd_{max}	Maximum attainable basal stem diameter increment in one time step (cm)	0.388 cm yr ⁻¹
d_{max}	Maximum attainable basal stem diameter (cm)	115.36 cm
h_{max}	Maximum attainable tree height (cm)	2055.05 cm
l_{max}	Maximum intensity of interaction	0.95
rbh	Basal stem radius	0.015±0.0015 m
Plot size		20 m x 20 m
Initial density	Density of trees placed in each plot at the beginning of the simulation	2500 ha ⁻¹
Initial distribution	Spatial distribution of trees at the beginning of each simulation	random
Propagules per m ² crown surface area	Number of propagules generated according to the crown surface area of each tree	0.15
Propagule weight	Average fresh weight of <i>A. germinans</i> propagules	1.1 g
Simulation runs	Number of repetitions of each simulation setting with different initial spatial distributions	20
Simulation time	Time span of each simulation run, simulation start corresponds to one year past	16 time steps (equivalent to 17 years)
Dispersal mode	Dispersal of propagules either in clustered in seed shadow of parent tree (short-range) or randomly and uniformly in plot (long-range)	short-range (Nat_Reg_Nat_Dis), long-range (Nat_Reg_Rand_Dis)
$l_{reduction}$	Reduction factor of Interaction intensity	0; 0.1; 0.2; 0.3; 0.4

dence of tree size at a distance r (Stoyan and Penttinen, 2000, p. 346). The mark correlation function $\kappa_{mm}(r)$ for quantitative marks is the conditional mean of the test function

$$\kappa_{mm}(r) : t(m_i, m_j) = m_i m_j \quad (4.11)$$

where m_i and m_j are marks of pairs of points which are normalized by the mean mark value (Illian et al., 2008, p. 346). If $\kappa_{mm}(r) = 1$, the size of tree attributes is independent at distance r apart and are not spatially correlated. If $\kappa_{mm}(r) > 1$ tree size is on average larger than the population's mean value and thus positively correlated at distance r . If $\kappa_{mm}(r) < 1$ tree size is on average smaller than the population's mean value and negatively correlated at distance r . Therefore, $\kappa_{mm}(r)$ shows whether trees which are separated by the distance r are of average size or smaller or larger than the average tree size.

The mark variogram $\gamma_m(r)$ is based on the test function

$$\gamma_m(r) : t(m_i, m_j) = \frac{1}{2} (m_i - m_j)^2 \quad (4.12)$$

i.e. the squared differences of mark pairs m_i and m_j at distance r apart and normalized by the mark variance (ibid., p. 344). If $\gamma_m(r) = 1$, the size of tree attributes is independent. If $\gamma_m(r) > 1$ attributes of neighboring trees are different in size (negative autocorrelation), whereas if $\gamma_m(r) < 1$ attributes are similar in size (positive autocorrelation) (Suzuki et al., 2008).

4.3 RESULTS

4.3.1 POINT PROCESS MODEL OF SEED DISPERSAL

The bivariate nearest neighbor function $G_{seedling-tree}(r)$ in Figure 4.5 shows that 70-80% of seedlings are located within 50 cm distance to the nearest tree stem and a small number of seedlings which were more distantly located than expected in a random distribution. This shift from aggregation to repulsion underlines the influence of a secondary dispersal process influences the spatial distribution of seedlings. One exception is plot 1A (2014) where all seedlings were aggregated around trees.

The comparison of the observed bivariate nearest neighbor distance distribution function $G_{seedling-tree}(r)$ with the two simulation envelopes generated by the

gravitational dispersal model and the tidal dispersal model revealed that the latter model could be fitted to all observed seedling patterns. Only in plot 3A (2011) was the gravitational seed dispersal model less suitable to describe seedling distribution in close proximity to neighboring tree stems. The gravitational dispersal model was inappropriate to describe seed dispersal in all other plots. The maximum range of simulated gravitational dispersal is much lower than the observed seedling distribution. Furthermore, the simulated gravitational dispersal pattern is more strongly clustered around trees.

Figure 4.5 also shows how the parameters mean crown radius, dispersal distance and dispersal probability influence the spatial distribution of seedlings around tree stems. Larger mean crown radii result in more randomly distributed seedling patterns as the maximum distance between seedlings and trees aligns with a Poisson distribution. The tidal dispersal distance increases the maximum distance at $G(r)$ at $r = 1.0$ set by the gravitational dispersal, whereas a higher probability of tidal dispersal creates a more random distribution. Therefore, both crown radius and seed dispersal probability determine the aggregation intensity of seedlings.

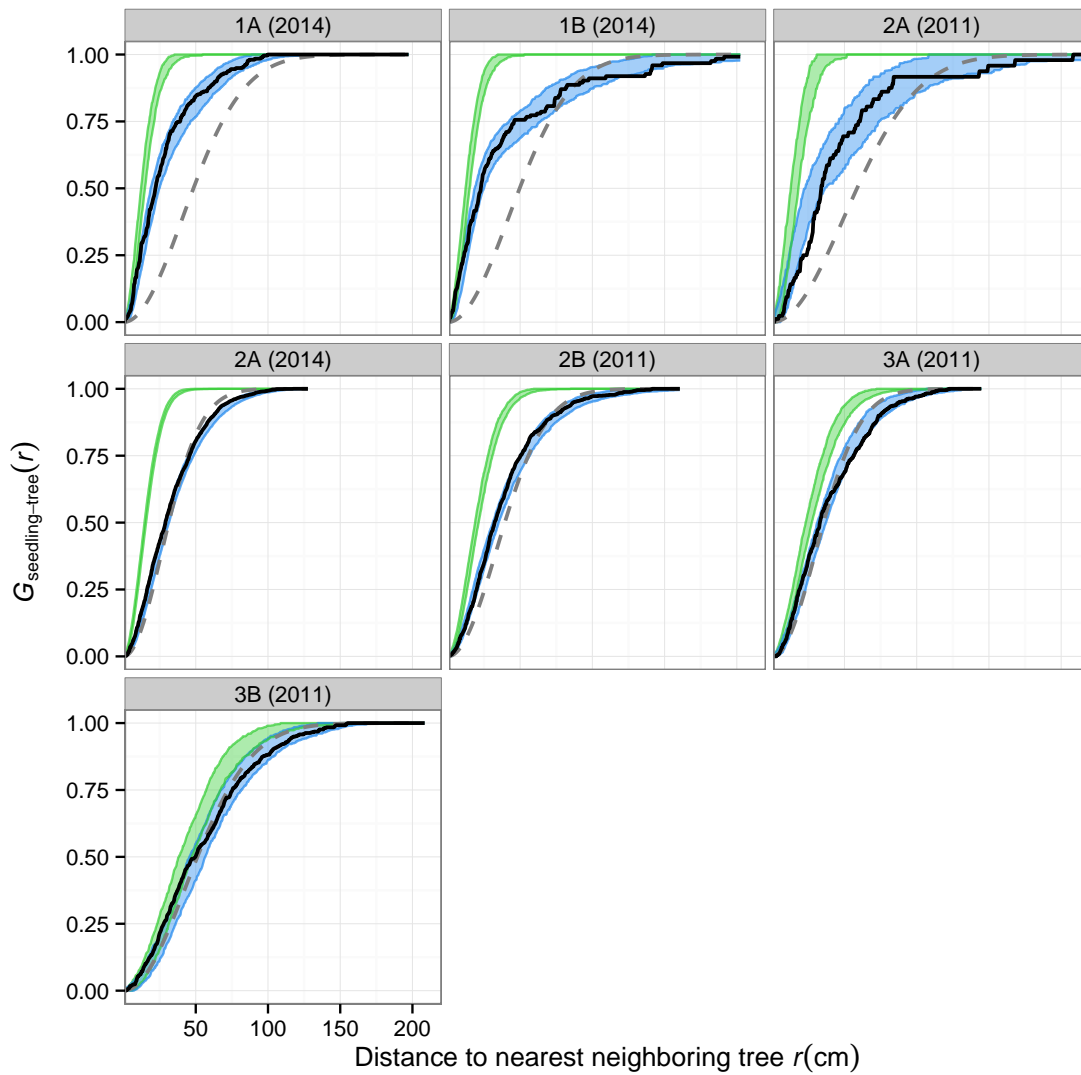


Figure 4.5: The bivariate nearest neighbor distribution function $G_{seedling-tree}(r)$ indicates the probability of a seedling having its nearest neighboring tree at distance r . The observed seedling-tree association is indicated by a black solid line. The grey dashed line delineates the theoretical value for a random distribution with the same intensity. The green envelope is based on 199 simulated point patterns of the Thomas point process model of gravitational seed dispersal. The blue envelope is based on the Thomas point process model combined with subsequent perturbation process of tidal seed dispersal.

Table 4.2 summarizes the dispersal parameters which resulted in the best model fit and reflect the maximum distance of tidal dispersal and probability of tidal seed dispersal in each plot. On average $67.1 \pm 12.5\%$ of landed seeds are transported up to a range of 307.1 ± 105.8 cm by tidal currents before settling.

Table 4.2: Parameters of random perturbation process (maximum dispersal range) and random labeling process (dispersal probability) which resulted in the best fitting point process model of tidal propagule dispersal compared to the observed seedling distribution.

Plot (Year of measurement)	Mean crown radius (cm)	Max. dispersal range (cm)	Dispersal probability (%)
1A (2014)	10.9	100	60
1B (2014)	10.4	300	50
2A (2014)	13.3	350	90
2A (2011)	11.3	250	60
2B (2011)	19.8	400	70
3A (2011)	32.4	400	70
3B (2011)	58.4	350	70

4.3.2 POINT PROCESS MODEL OF SEEDLING ESTABLISHMENT

Subsequently to the point process modeling of seed dispersal, the influence of trees on the spatial distribution of seedling establishment was modeled. In the plots with relatively low tree and seedling density, 1A (2014), 1B (2014) and 2A (2011), all three thinning models resulted in very similar and almost indistinguishable spatial patterns. Therefore, a competitive, facilitative and independent influence of trees on seedling establishment resulted in the same aggregated point pattern. This means that the observed seedling-tree pattern could not be attributed to a single process. In the other plots, simulation envelopes based on $g_{seedling-tree}(r)$ were differentiable at close proximity to the nearest tree stem ($r = 0$) in the radius of the ZOI (Figure 4.6). Observed seedling-tree patterns were generally located between simulation envelopes based on facilitative and independent thinning simulations. The spatial pattern generated by a competitive thinning simulation deviated most strongly from the observed pattern compared to the other models. This shows that seedling establishment was not negatively influenced by neighboring trees following seed dispersal but either independent or positively influenced by neighboring trees.

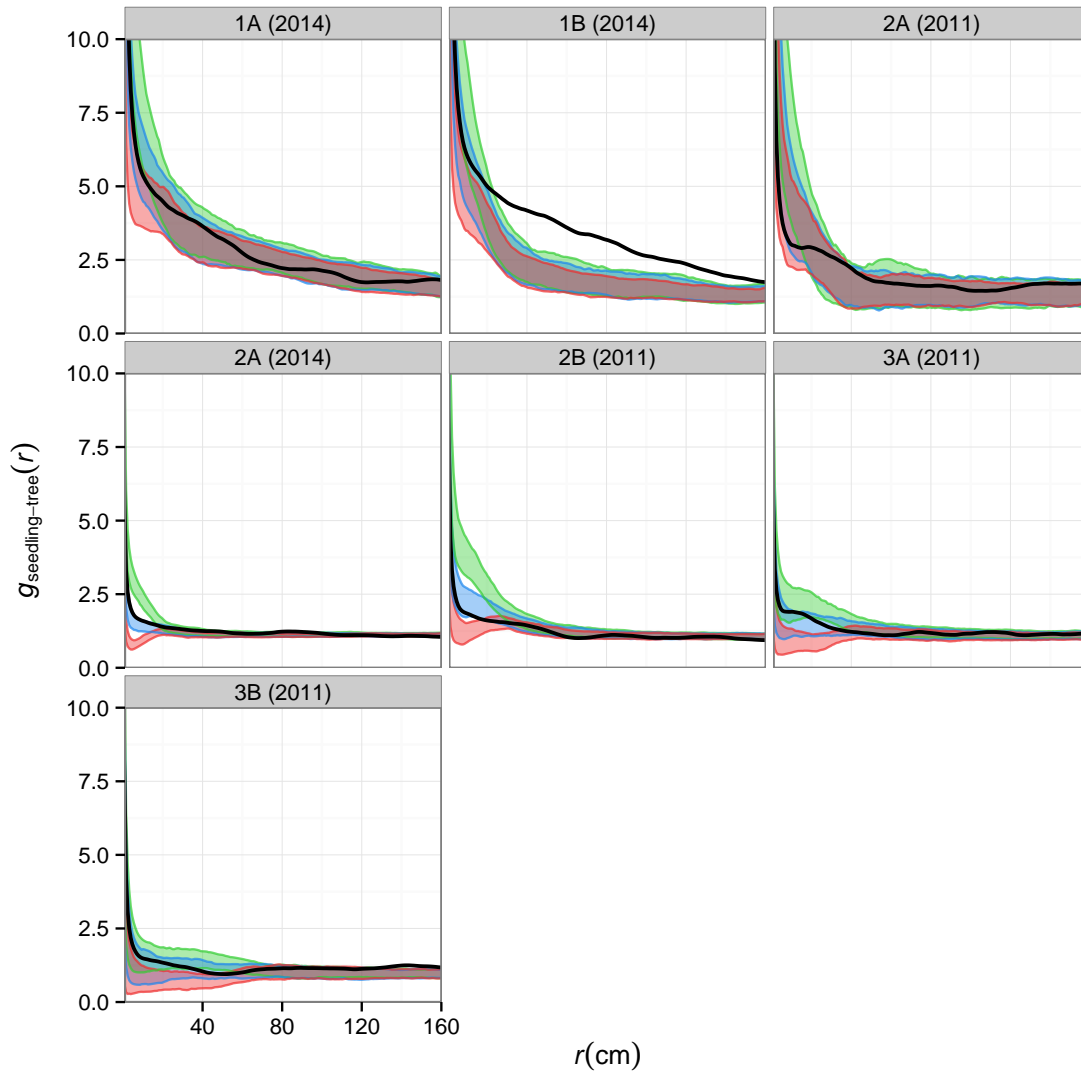


Figure 4.6: Goodness-of-fit of the combined point process model of tidal dispersal and seedling establishment (simulation envelopes) to the observed seedling distribution around trees (black solid line) based on the bivariate pair-correlation function $g_{seedling-tree}(r)$ at distance r . The blue envelope represent the simulated realizations of a thinning procedure of seedlings which is independent of trees. The green envelope represents the point pattern resulting from a facilitative influence of trees on seedlings, whereas the red envelope represents a competitive influence of trees.

I conducted two sensitivity analyses of the seedling establishment model to analyze how much the variation of both dispersal parameters, dispersal distance (Figure 4.8) and probability (Figure 4.7), influence the simulation envelopes of the independent seedling establishment model. Both figures show that the simulation envelope generated after a variation of each parameter does not differ from the original simulation in Figure 4.6, which is shown in each sensitivity analysis as dashed line (Figure 4.8, 4.7).

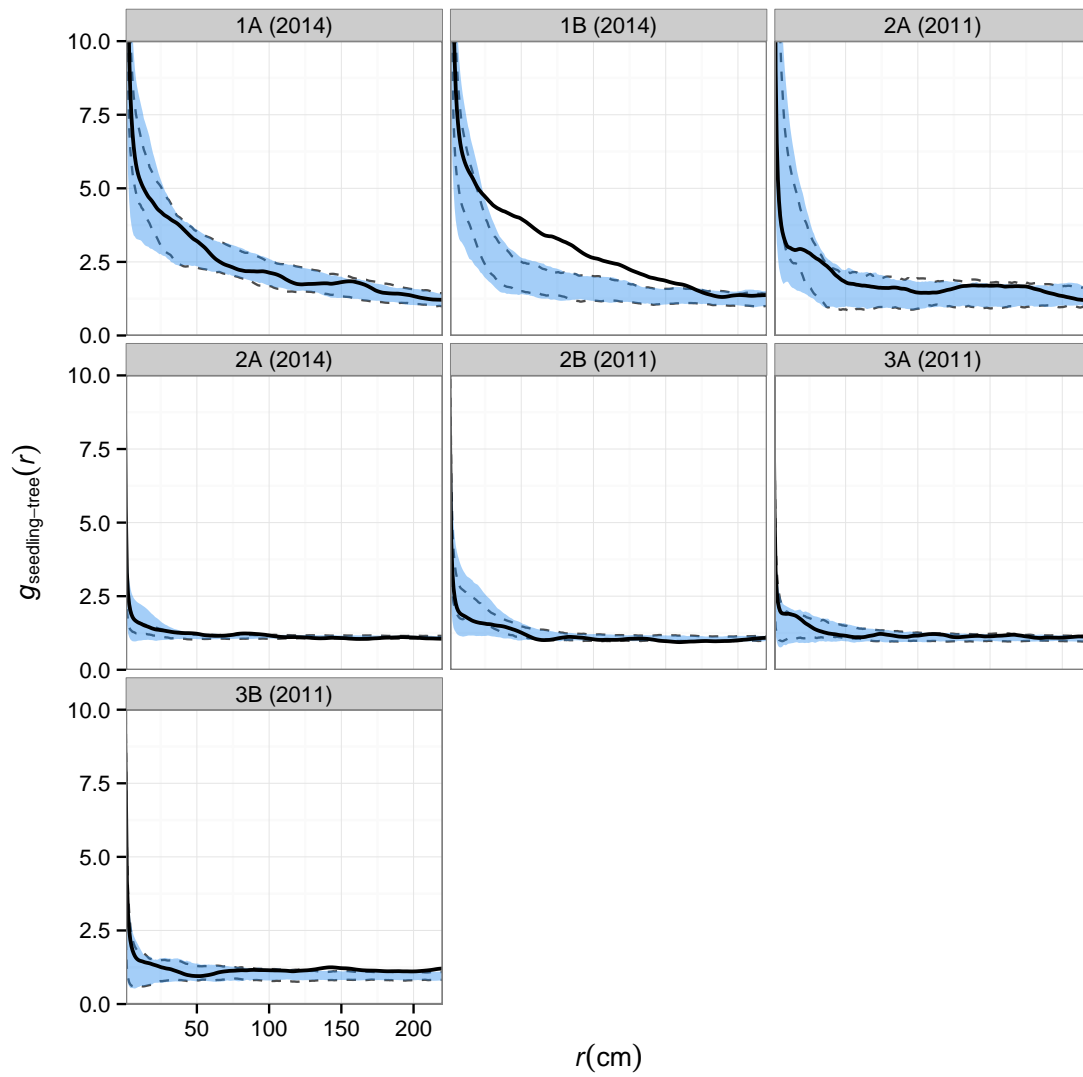


Figure 4.7: Sensitivity of the independent seedling establishment model to a variation of tidal dispersal probability by $\pm 20\%$ assessed by the bivariate pair-correlation function $g_{\text{seedling-tree}}(r)$ at distance r (blue). Dashed lines delineate the simulation envelope created by the independent thinning model without variation of the dispersal parameters.

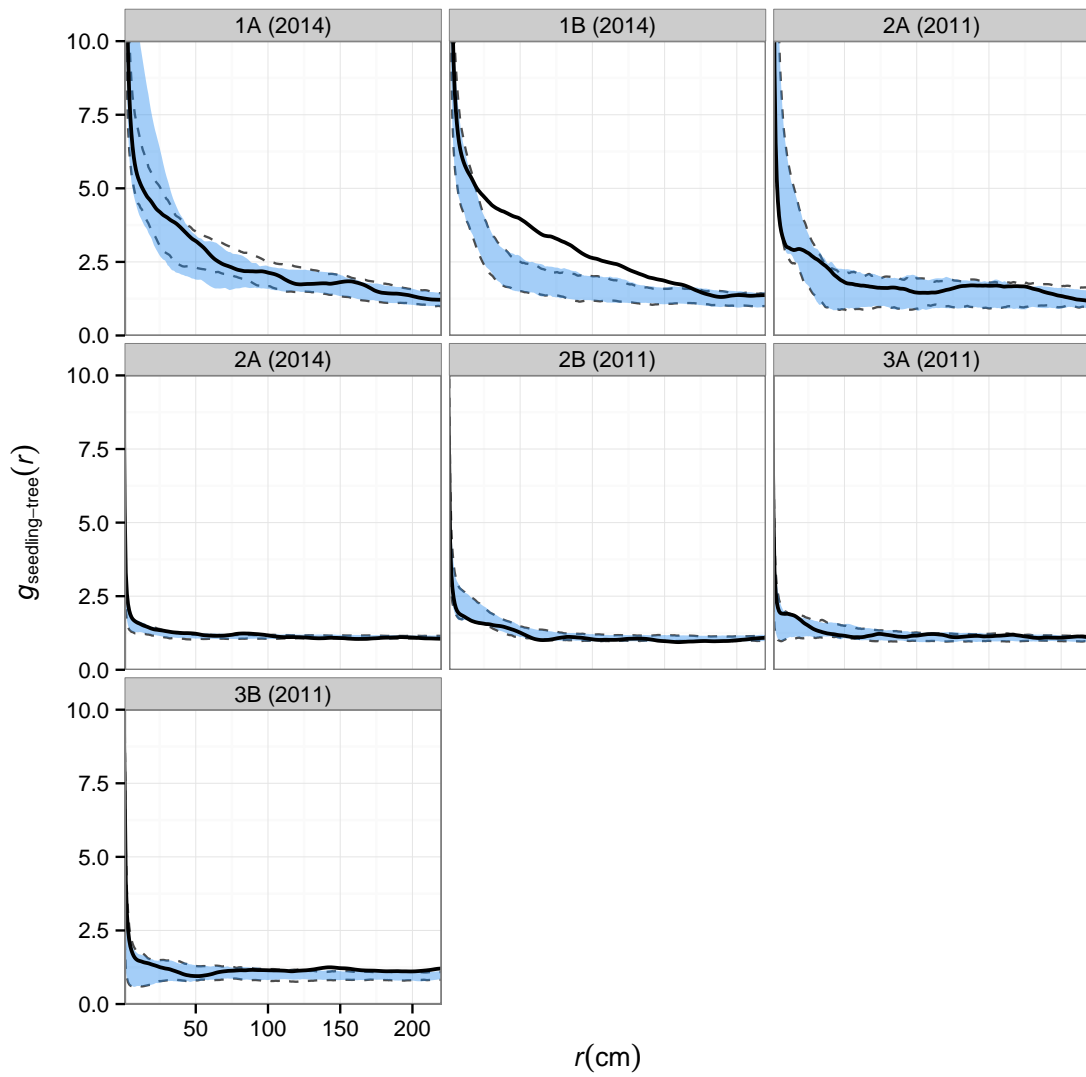


Figure 4.8: Sensitivity of random thinning model to a variation of tidal dispersal distance by ± 100 cm assessed by the bivariate pair-correlation function $g_{seedling-tree}(r)$ at distance r (blue). Dashed lines delineate the simulation envelope created by the independent thinning model without variation of the dispersal parameters.

4.3.3 INDIVIDUAL-BASED MODEL OF TREE INTERACTION

In the following, point patterns generated with the individual-based mangrove model mesoFON are presented. The pair-correlation function $g(r)$ showed that despite a change from competitive to facilitative tree interaction (I_{max}) the spatial distribution of trees remained random when seeds were dispersed randomly (Figure 4.9). In contrast, trees were consistently clustered under the influence of short-range seed dispersal regardless of the level of tree interaction. As density increases with progressing simulation trees cluster less strongly regardless of the level of tree interaction. This means that the pair-correlation function did not show any signs of competitive or facilitative tree interaction.

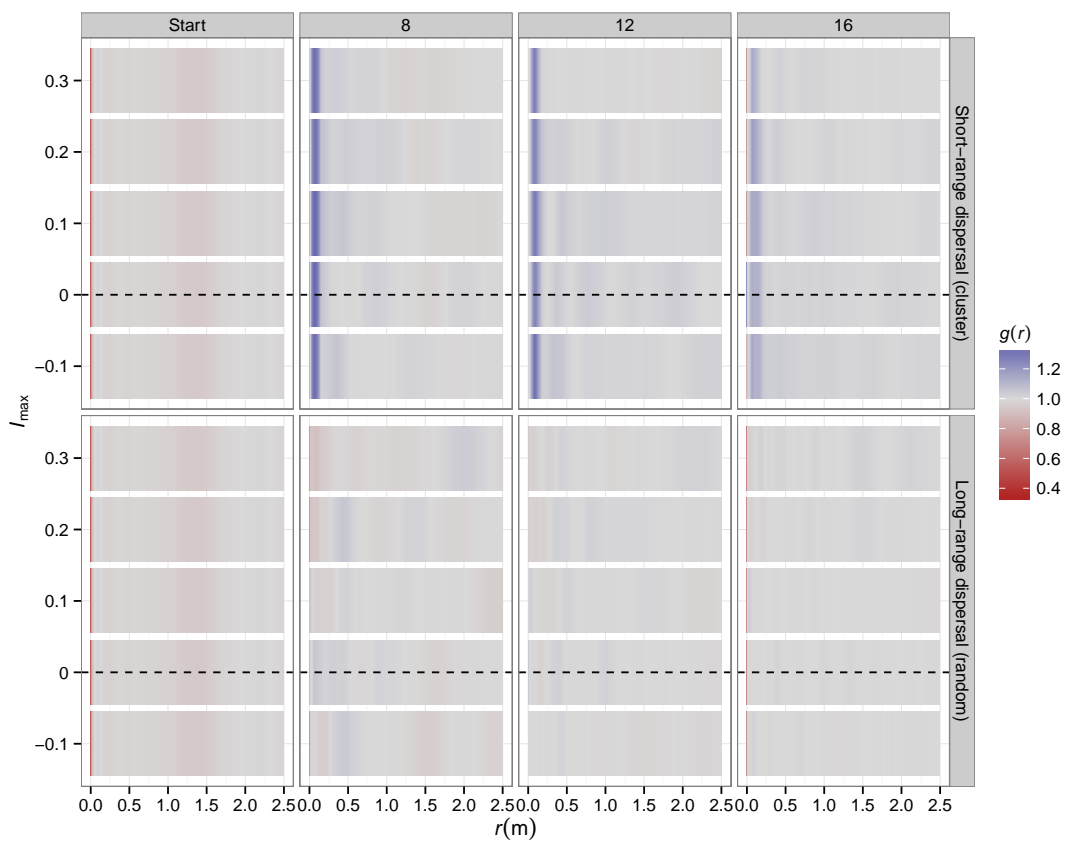


Figure 4.9: Spatial tree distribution at different levels of interaction I_{max} and two dispersal mechanisms (short-range and long-range seed dispersal) at the simulation start and at time steps 8, 12 and 16 based on the pair-correlation function $g(r)$. Colors indicate magnitude of $g(r)$ at distance r . Values above 1 (blue) indicate tree clustering at distance r , values below 1 (red) indicate tree regularity at distance r .

The mark-correlation function $\kappa_{mm}(r)$ is used to analyze the dependence of tree height on the distance between trees (Figure 4.10). Regardless of the mode of propagule dispersal, the mark-correlation function showed a shift from negative towards positive mark correlation corresponding to the mode of tree interaction set by I_{max} . Moreover, the strength of mark correlation increased with each time step. At a balanced level of positive and negative tree interaction ($I_{max} = 0$) tree marks are uncorrelated and not influenced by their neighbors.

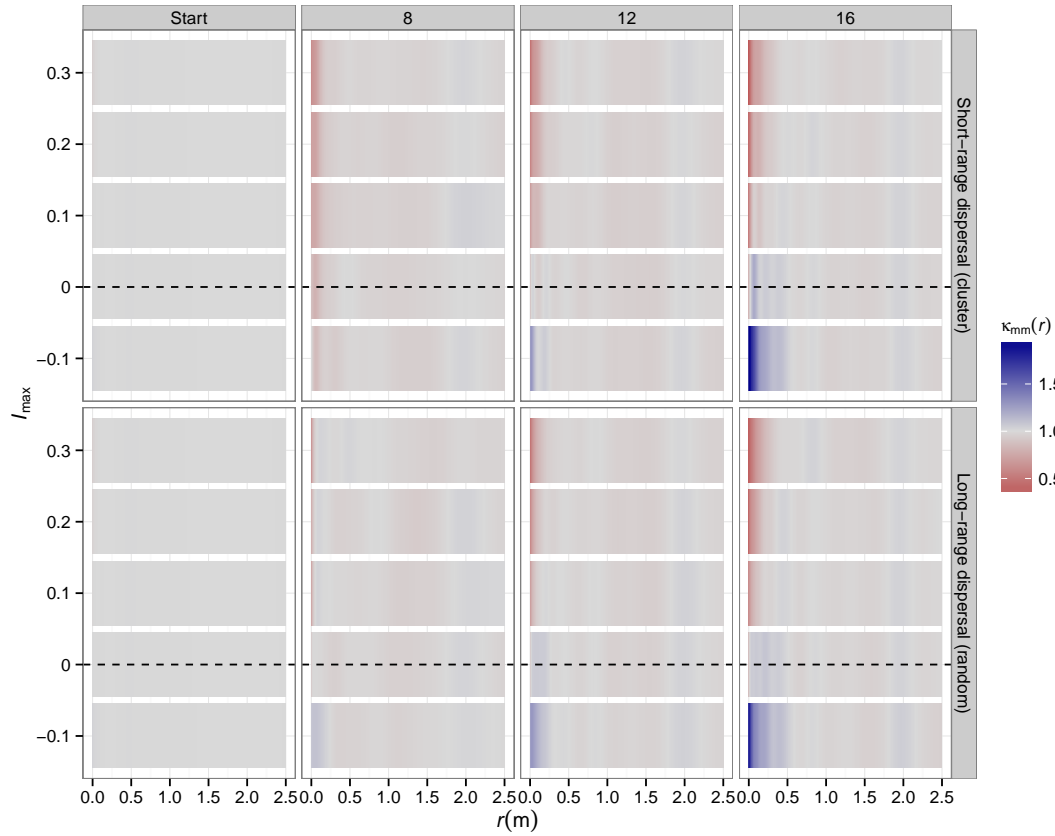


Figure 4.10: Spatial tree height distribution at different levels of interaction I_{max} and different dispersal mechanisms (short-range and long-range seed dispersal) at the simulation start and at time steps 8, 12 and 16 based on mark-correlation function $\kappa_{mm}(r)$. Colors indicate magnitude of $\kappa_{mm}(r)$ at distance r . Values above 1 (blue) indicate positive size correlation at distance r , values below 1 (red) indicate negative size correlation at distance r .

The mark variogram $\gamma_m(r)$ is used to analyze the relationship between tree size and tree distance (Figure 4.11). All initial distribution show a positive autocorrelation as the initial tree size was set to a mean dbh of 1.5 cm with a standard deviation of 0.15 cm. Under random dispersal, size difference between trees was independently distributed. At short-range dispersal, the size difference among trees increased although the magnitude of dissimilarity decreased with more competitive interaction. The size dissimilarity was highest under the influence of short-range propagule dispersal and positive tree interaction ($I_{max} = -0.1$). The mark variogram did not detect any differences between levels of tree interaction under long-range dispersal.

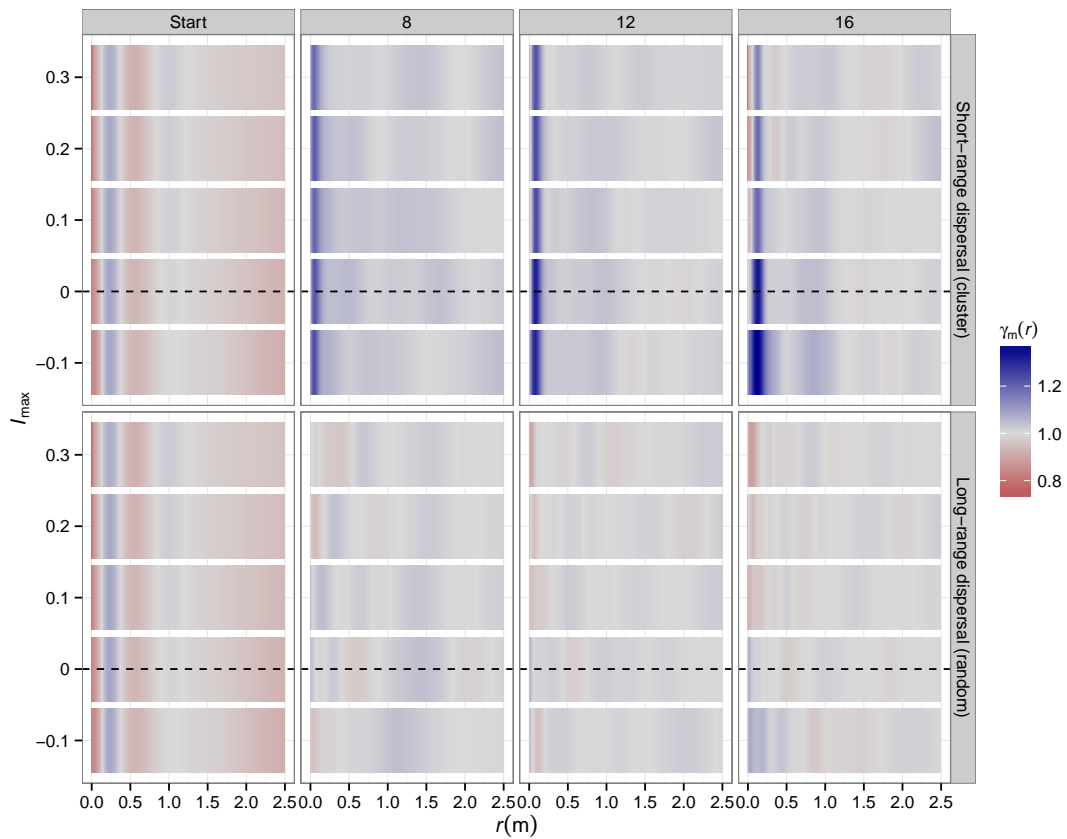


Figure 4.11: Spatial tree height differentiation at different levels of interaction I_{max} and different dispersal mechanisms (short-range and long-range seed dispersal) at the simulation start and at time steps 8, 12 and 16 based on normalized mark variogram $\gamma_m(r)$. Colors indicate magnitude of $\gamma_m(r)$ at distance r . Values above 1 (blue) indicate size dissimilarity at distance r , values below 1 (red) indicate size similarity at distance r .

4.4 DISCUSSION

Point pattern analysis is a useful tool for revealing the presence of past or current ecological processes which are difficult to detect directly. However, various processes can produce similar or identical spatial patterns. In the case of monospecific plant communities, aggregated plant distributions can be the result of short-range seed dispersal and facilitative interactions, such as nurse-plant effects, or both processes. In the first part of this study, I developed a complex point process model to disentangle these two processes and investigate their presence in a recolonizing *A. germinans* mangrove forest. I found strong evidence that the observed aggregation of seedlings around trees is the result of gravitational and tidal dispersal processes, and less likely generated by nurse-plant effects.

In the second part, I employed the individual-based mangrove model meso-FON to investigate the appropriateness of the mark-correlation function and mark variogram for the detection of competitive and facilitative interaction among conspecific *A. germinans* trees. The results revealed that the mark-correlation function is a suitable summary statistics to detect positive and negative interaction among trees by analyzing the spatial distribution of tree size attributes.

4.4.1 HOW FAR WERE *A. GERMINANS* PROPAGULES DISPERSED BY TIDAL CURRENTS?

Release and recapture experiments were conducted to measure the dispersal distance of various mangrove species from seaward zones to other coastal areas (Clarke, 1993). These experiments showed that, in general, propagules can be dispersed over a distance of up to several kilometers, but the majority strands within a range of a few hundred meters (ibid.). Dwarf mangrove forests are often located along the inland boundary of a mangrove ecosystem and shaped by infrequent inundations and low water levels (Lovelock and Feller, 2003). This inundation regime is likely to limit widespread dispersal of buoyant propagules to smaller areas. Therefore, propagule dispersal should be even more localized within landward mangrove forests compared to more seaward forests. I applied a point process modeling approach to estimate two factors of propagule dispersal, distance and probability of tidal dispersal instead of conducting similar release and recapture experiments.

The dispersal simulation suggests that around 67% of propagules are displaced within a radius of up to 3 m after parting from their parent tree. Moreover, 33% of all dispersed propagules establish within the seed shadow be-

cause these propagules do not experience any inundation until they are entirely rooted and cannot be displaced. In a release and recapture experiments of *Ceriops tagal* propagules in high-shore areas, McGuinness (1996) found that 91% of all propagules settled within 3 m from the parent tree. This confirms that the dispersal range of mangroves in less frequently inundated areas is very limited.

These results represent average estimates from 7 plots studied within an infrequently inundated *A. germinans* forest. The findings also show that there are deviations among forest plots, which are most likely caused by micro-topographical variations in the study area. The mapped forest plots represent multiple realizations of underlying ecological processes and provide a better approximation of the real dispersal and interaction parameters than only one observation plot would provide.

Seedlings were aggregated around trees in all plots. This aggregation is created by infrequent inundations and not the result of limited dispersal distances. A random seedling pattern would be created if all propagules would be displaced even within a small radius. If only a limited number of propagules would be dispersed hydrochorously the aggregated spatial distribution of seedlings would be maintained.

There are several factors which determine the probability of a landed propagule being dispersed further by tidal current before their final settlement. First, *A. germinans* produces propagules over a period of 5 months (Menezes et al., 2008) during which propagules can experience very different tidal conditions. *A. germinans* propagules require 7 days for rooting (Rabinowitz, 1978a). Second, abscission of *Avicennia* propagules from their parent trees might occur especially during low tides as observed in eastern Australia (Clarke and Hannon, 1971). Third, *A. germinans* propagules differ in their buoyancy as observed by McKee (1995b) who found that 92.3% float whereas 7.7% sank in seawater.

4.4.2 HOW IS THE ESTABLISHMENT OF *A. GERMINANS* SEEDLINGS INFLUENCED BY NEIGHBORING TREES?

Propagules settle after their dispersal in a microhabitat which regulates their subsequent survival, growth and development (Harper, 1977). In certain microhabitats, harsh environmental conditions may limit propagule survival and seedling establishment (Clark et al., 2013). Some studies observed the beneficial effect of nurse plants which improve the growing conditions of surrounding seedlings by ameliorating environmental stress, hence seeds may be more likely to survive and root under the canopy shelter of nurse plants (Gómez-Aparicio et al., 2005b; Maestre et al., 2001; Pugnaire et al., 1996). Other studies

did not observe this form of facilitation in harsh environments (Maestre et al., 2005; Maestre et al., 2009; Tielbörger and Kadmon, 2000). Therefore, the observed aggregation of *A. germinans* seedlings around conspecific trees may be the result of short-range seed dispersal processes or evidence of nurse-plant interactions between *A. germinans* trees and seedlings (Ledo et al., 2014).

I combined the fitted dispersal point process simulation with a thinning model in order to further investigate the bivariate association of seedlings and trees and to disentangle intraspecific facilitation from seed dispersal limitations. The tidal dispersal model was fitted to describe the observed maximum distance between seedlings and trees, whereas the thinning model was used to explore the interaction between seedlings and trees at a short distance, usually the distribution of seedlings within the mean crown radius.

The fit of the observed seedlings distribution to the independent seedling establishment model indicates that the spatial pattern of post-dispersal seedling establishment is independent of the influence of trees. Therefore, trees neither influence the survival of propagules nor the rooting of young seedlings positively or negatively. The aggregation of seedlings around trees is the result of gravitational and tidal dispersal processes. The sensitivity analysis demonstrated that the seedling establishment model is not sensitive to the fitted dispersal parameters, i.e. a deviation of the actual tidal dispersal from the fitted parameters would not change the interpretation of the seedling establishment model.

Mangrove seedlings are very susceptible to harsh environmental conditions (Krauss et al., 2008). McKee (1995b) observed that desiccation accounted for 41% of *A. germinans* propagule mortality in elevated mangrove forests. In a laboratory experiment, McMillan (1971) found that young *A. germinans* seedlings died after a forty-eight-hour exposures to 39–40°C. Therefore, I suggest that the results of this study do not indicate that *A. germinans* propagules and seedlings in this area are unusually robust and can withstand harsh environmental conditions. It is more likely that trees are not able to ameliorate these stress factor sufficiently to act as nurse plants and enhance seedling establishment in their vicinity.

However, based on these results I cannot reject a possible nurse-plant effect of trees on the subsequent survival and growth of seedlings beyond establishment. In order to investigate this possible interaction between trees and seedlings, information about the size, growth or mortality of each seedling is required in order to conduct a bivariate mark-correlation analysis and to find out how the distance to neighboring trees is associated with seedling growth and development (Martinez et al., 2013; Wiegand and Moloney, 2013, p. 220).

4.4.3 ARE SPATIAL SUMMARY STATISTICS SUITABLE TO DETECT THE EFFECT OF INTERACTION ON TREE SIZE UNDER THE INFLUENCE OF SHORT-RANGE SEED DISPERSAL?

In the second part, I simulated the early development of an *A. germinans* forest using the mesoFON model. The individual-based model enabled me to investigate the influence of two simultaneous processes, seed dispersal and intraspecific interaction, on the spatial pattern and the appropriateness of spatial summary statistics to detect these underlying processes. In the simulation experiment, I gradually altered the level of tree interaction from competition to facilitation which resulted in a shift from negative size correlation to positive size correlation. Thus, trees benefited from their neighbors through higher growth rates. The goal of this study was not to investigate how intraspecific interaction affects tree growth (see chapter 3) but to analyze the appropriateness of commonly used spatial summary statistics.

The results of the mark-correlation function indicate facilitation and competition interaction irrespective of dispersal distances. Therefore, the mark-correlation function was appropriate to detect different levels of tree interaction both in short-range clustered seed dispersal and long-range random seed dispersal. In addition, static tree attributes, such as tree height or diameter, can provide sufficient insights about the level of interaction comparable to dynamic, tree growth attributes.

The mark variogram revealed that short-range seed dispersal resulted in a negative autocorrelation, hence the size of neighboring trees is different. This size-dissimilarity can be observed in all levels of tree interaction.

In contrast to the mark-correlation function, the pair-correlation function only detects differences in dispersal processes but not the effect of interaction levels. It is likely to see the self-thinning processes as forest development progresses, which would differentiate the spatial pattern under the influence of different levels of interaction. However, in this simulation experiment competition rarely caused tree mortality which corresponds to the observed *A. germinans* forest stand. Therefore, marked point patterns are required for the analysis of tree interactions in forest stands which are not experiencing self-thinning processes.

4.5 CONCLUSION

Point process modeling was used to analyze whether the clustered spatial distribution of seedlings around *A. germinans* trees was a result of short-range

seed dispersal, nurse-plant effects, or both. The fitted complex point process model suggested that around 67% of propagules were displaced during tidal inundations. The establishment of the remaining propagules in the seed shadow of their parents explained the resulting clustering of seedlings around trees. However, seedling establishment was not influenced positively or negatively by trees. This result suggests that trees were too small to ameliorate environmental conditions in their surrounding and affect seedling establishment. The results of the individual-based model mesoFON revealed that marked point patterns, which were analyzed using mark-correlation function, can provide detailed insights regarding the effect of tree interaction on size and growth. The effect of trees on seedling establishment and development could be studied in more detail by analyzing seedling size and growth as well.

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5 CONCLUDING DISCUSSION

Annually 150,000 ha of degraded and destroyed mangrove forest worldwide need to be restored in order to compensate continuous mangrove deforestation which exceeds the average rate of global deforestation by three to five times (Bosire et al., 2008; FAO, 2007). However, our knowledge of the underlying ecological processes of mangrove forest regeneration is too limited in order to develop suitable techniques for the restoration of severely degraded mangrove areas (Gedan and Silliman, 2009; Primavera and Esteban, 2008). In this dissertation I investigated the regeneration dynamics and tree interaction of *Avicennia germinans* following a stand-replacing event using point pattern analysis and point process modeling.

5.1 MAJOR FINDINGS

In infrequently inundated areas, 67% of *A. germinans* propagule were further dispersed by tidal currents in a maximum range of approximately 3 m around their parent tree, whereas 33% established in the seed shadow of their parent trees (chapter 4). Limited dispersal has been observed in other mangrove forests with differently shaped propagules as well. McGuinness (1996) observed in a release and recapture experiment in a high shore environment that the torpedo-shaped propagules of *Ceriops tagal* were also dispersed within a range of 3 m around their parent tree.

The results of chapter 2 showed that crown cover had a positive effect on seedling density which suggests that *A. germinans* trees did not suppress the establishment of conspecific seedlings under harsh environmental conditions. However, the point process model in chapter 4 revealed that this positive association of seedlings under crown cover is caused by short-range seed dispersal

due to infrequent tidal inundations and a result of intraspecific nurse-plant effects of trees increasing seedling establishment and survival. In contrast, coarse wood debris had no apparent effect on seedling establishment.

The high density of *A. germinans* seedlings and recruited trees in patches of the herbaceous salt-marsh plants *Blutaparon portulacoides* and *Sesuvium portulacastrum* suggests that inter-specific interaction has a facilitative effect on mangrove trees which goes beyond the seedling stage. This shows that herbaceous vegetation does not only entrap propagules (McKee et al., 2007; Milbrandt and Tinsley, 2006; Peterson and Bell, 2012) but could also ameliorate environmental conditions for tree recruits.

In chapter 3, the effect of tree interaction on the size and growth of shrub-like *A. germinans* trees was studied in detail. Under these harsh conditions trees with less growing space and more neighbors were taller and had longer internodes. However, in more sparse forest plots (1.2 tree m⁻²) was the facilitative effect of tree interaction stronger than in denser areas (2.7 trees m⁻²). This suggests a shift from facilitation to a balance of competitive and facilitative tree interaction with increasing tree density. In denser plots, trees were under more pressure from neighboring trees and avoided competition through crown displacement. However, crown displacement was not associated with a negative effect on tree growth.

5.2 EVALUATION OF SPATIAL POINT PATTERN STATISTICS

Spatial point pattern analysis and modeling was used to extract information from observed spatial pattern and to infer underlying processes from plant distributions.

The measured trees were not only described by their position but also by their size which constitutes a marked point pattern. The mark correlation function $\kappa_{mm}(r)$ was used to analyze the spatial size-correlation of the tree size attributes based on the distance r between tree stems and thus provides information about relationship of tree interaction and tree size (Stoyan and Penttinen, 2000, p. 346). The simulation study in chapter 4 showed that the mark-correlation function is an appropriate method for detecting positive and negative tree interaction and can be even used with tree size information instead of growth data. The results of the mark-correlation function revealed different levels of tree interaction regardless of short-range or long-range seed dispersal processes. In contrast, the mark variogram was strongly influenced by dispersal processes and did not

consistently detect tree interaction levels as the mark-correlation function did. Accordingly, I applied the mark-correlation function in chapter 3 to analyze how tree interaction affects tree growth and size.

In chapter 3, I also analyzed the relationship of tree interaction and size using a linear regression. I described tree interaction intensity by calculating the potentially available growing space based on a Dirichlet tessellation of the forest plot. By employing a tessellation approach to quantify the neighborhood density of a focal tree I did not rely on distance-dependent competition indexes which were unsuitable to describe the relationship of tree interaction and tree size. It described sufficiently the neighborhood density of isolated trees as well as trees in dense areas. Contrary to common competition indexes, it does not correlate with tree size.

In chapter 2 and 4, point process models were developed and used to fit suitable parameters which generate a point pattern similar to the observed pattern (Wiegand et al., 2007; Wiegand et al., 2009).

Gibbs point process models were used in chapter 2 to analyze the dependence of seedling and tree position on multiple spatial and numeric covariates as well as interaction processes (Baddeley, 2008). Each Gibbs model was fitted to three point patterns based on mappings of three forest plots. The goal was to develop a more robust model and to detect differences between forest plots in the dependence of seedlings and trees on covariates. The goodness-of-fit as well as the sensitivity of each Gibbs model was analyzed with the R-package spatstat (Baddeley and Turner, 2005; Baddeley et al., 2005).

Thomas point process models were used in chapter 4 to simulate gravitational dispersal processes. Furthermore, I applied a random perturbation process to the generated point pattern in order to simulate tidal dispersal. This complex point process model was used to simulate different tidal regimes and to fit the resulting point distribution to the observed seedling pattern. However, I could not use model-fitting algorithms due to combination of different point processes. Thus, I relied on a visual comparison of the simulated and observed seedling pattern. This dissertation demonstrated that Thomas point process models can complement release and recapture experiment in the study of regeneration processes (Seidler and Plotkin, 2006; Wiegand et al., 2007).

5.3 MANAGEMENT IMPLICATIONS FOR MANGROVE RESTORATION

Natural mangrove recolonization and regeneration often occurs at a slow pace, and the re-establishment of the original natural mixed mangrove forest might take decades if not centuries (Osland et al., 2012). Although mangrove restoration is often focused on planting (Primavera and Esteban, 2008), mangroves can colonize naturally large mudflat and salt-marsh areas without extensive human intervention (Peterson and Bell, 2012; Proisy et al., 2009). The natural regeneration of a site can be assisted by removing two limitations, first, a limited supply of propagules and, second, unsuitable site conditions limit germination and seedling establishment (Clark et al., 1999a).

The influx of propagules from well-developed mangrove stands to neighboring degraded areas might be obstructed by artificial structures which disturb tidal inundations. The local hydrology should always be restored prior to a mangrove restoration if possible (Field, 1999). A limited propagule supply could be also the result of a complete absence of mature mangrove stands. In this case, planting is required to re-establish a mangrove population. Propagule trapping structures, such as ground-covering vegetation, which entrap mangrove propagules after they were transported by tidal inundations landwards play an important role in the regeneration of mangrove forests. Without entrapment structures propagules would enter the degraded site with a tidal inundation and would be drawn back afterwards (Peterson and Bell, 2012).

The planting of nurse plants and herbaceous vegetation in degraded mangrove forests has the potential to solve the problem of severe mortality among planted seedlings (Gedan and Silliman, 2009). Instead of weeding prior to planting mangrove seedlings, I suggest to assist natural regeneration by preserving or planting patches of salt-marsh plants. Although my results have shown that seedling density was lower in patches of *S. portulacastrum* than in patches of *B. portulacoides*, *S. portulacastrum* had a sustained positive effect on post-dispersal tree recruitment. Therefore, herb cover provided a starting point for recolonization in low-density forest stands and had no negative impact on mangrove regeneration.

Overcoming the establishment barrier caused by unfavorable site conditions is often more challenging than planting seedlings. Many factors can result in high seedling mortality and the failure of restoration projects (Primavera and Esteban, 2008). The selection of the suitable mangrove tree species is one crucial decision and this research showed that *A. germinans* is one mangrove tree species, which is able to thrive under these harsh conditions. Although most

trees were able to survive, the results of chapter 3 showed that the interaction of neighboring trees had a positive interaction on their growth in sparse forest stands. I suggest to plant seedlings or saplings in clusters instead of planting seedlings evenly spaced in order to utilize this beneficial effect. The objective of cluster plantings would not be to produce timber, but to reduce the mortality rate of seedlings until they reach their reproductive age in order to assist the natural regeneration in unplanted areas. Cluster planting has been utilized in mangrove restoration (Saint Paul, 2013) but it has not been studied in detail yet. The results could not conclusively show that shrub-like *A. germinans* trees exert a nurse-plant effect on the establishment of conspecific seedlings. However, further studies are needed to analyze whether trees facilitate the growth of neighboring seedlings.

5.4 RESEARCH OUTLOOK

Spatial point analysis should be understood as an exploratory method. The results which indicated facilitative interaction among trees, seedlings and herbs (chapter 2 and 3) should be further investigated with experiments. An experimental study would be useful to investigate how different tree life-stages, such as seedlings, saplings and trees, interact under different levels of environmental stress, for example salinity or soil moisture. An interesting aspect would be also to study whether the underlying mechanism of facilitative interaction is caused by direct shading of the plant itself or indirect shading of surrounding ground areas. Therefore, I propose a factorial field experiment to investigate how mangrove seedlings, saplings and trees react to different levels of direct shading, which are simulated by shade cloth located above the plant, and indirect shading by covering only the surrounding ground area under different levels of environmental stress. This experiment could also be applied to investigate the mechanism behind the beneficial effects of ground-covering herbs on seedlings and trees (Milbrandt and Tinsley, 2006).

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APPENDIX

PARAMETER OPTIMIZATION OF MESOFON

Genetic algorithms are population-based search algorithms which are used to find creative solutions to a parameter search problem (Stonedahl and Wilensky, 2011). They are computational processes which imitate evolutionary processes (Goldberg et al., 1989), and are increasingly applied for parameter optimization in individual-based models (Calvez and Hutzler, 2005; Stonedahl and Wilensky, 2011).

Genetic algorithms explore all possible solutions through mutation and optimize through selection and crossover of best solutions. Mutation of genes is applied to search for possible parameter solutions, i.e. in the exploration process parameter genes are assigned random values within the predefined range. The mutation rate defines the fraction of genes to be permuted randomly. Selection and crossover between chromosomes are applied to optimize solutions, i.e. genes are exchanged between two parent chromosomes to form two offspring chromosomes with a possibly better solution. The crossover rate defines the fraction of the chromosome population to be exchanged.

In order to study recolonizing *A. germinans* forests, the mesoFON model was parameterized to the growth of *A. germinans* under extreme environmental conditions using field data collected in plot 2A in 2011 and 2014. The optimization of 7 parameters (Table 5.1) was conducted based on generational genetic algorithms with a population size of 50, maximum number of 60 generations, a mutation rate of 1/20, and a crossover rate of 1/2, applying a tournament selection with a tournament size of 2 and a probability of 0.9 that the better chromosome wins.

The genetic algorithm was implemented using JGAP (Java Genetic Algorithm Package) by running the model with a population of genomes. Each genome

consisted of a vector of parameter genes

$$G = [a, b, \Delta d_{max}, d_{max}, h_{max}, asym, l_{reduction}] \quad (5.1)$$

where a (Equation 4.7 on page 109), b (Equation 4.7 on page 109), Δd_{max} (Equation 4.2 on page 108), d_{max} (Equation 4.1 on page 108), h_{max} (Equation 4.1 on page 108), $asym$ (Equation 4.9 on page 109), $l_{reduction}$ (Equation 4.6 on page 108) are model parameters.

mesoFON was started with tree positions and basal stem diameters, which were measured in plot 2A in the year 2011, irrespective of the genome being used in a model run. Each model run was stopped after 3 simulation years corresponding to the year 2014. The simulated basal stem diameters were compared with the basal stem diameters measured in 2014. The sum of the squared deviations between simulated and measured basal stem diameters was calculated and assigned as the fitness value to the respective genome. Afterwards the population of genomes was reproduced. In a tournament selection a certain number of genomes depending on the tournament size were randomly chosen and the fittest genome was transferred to the next generation according to a predefined probability. Tournament selection was repeated until the size of the original population is restored in the next generation.

Special attention was given to avoid premature convergence (a description of these routines is beyond the scope of this thesis). After many generations the fitness could not be minimized further and the set of parameters that fit the measured stem diameters best was obtained.

Table 5.1: List of optimized parameters with predefined range of parameter value.

Parameter	Range of values
a	9 - 14
b	0.5 - 0.8
Δd_{max}	0.3 - 0.63
d_{max}	40 - 140
h_{max}	400 - 3500
$asym$	0 - 0.5
$l_{reduction}$	0 - 1

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STATEMENT OF AUTHORSHIP

I hereby certify that I have authored this Dissertation entitled *Spatial patterns and processes in a regenerating mangrove forest* independently and without undue assistance from third parties. No other than the resources and references indicated in this thesis have been used. I have marked both literal and accordingly adopted quotations as such. During the preparation of this thesis I was only supported by the following persons:

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Additional persons were not involved in the spiritual preparation of the present thesis. I am aware that violations of this declaration may lead to subsequent withdrawal of the degree.

Tharandt, 05.03.2015

Aor Pranchai