

Patterns and individual-based
modeling of spatial competition within
two main components of Neotropical
mangrove ecosystems.

Doctoral thesis
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To my Parents, Martha and my future baby...

Preface

I have “really” started being interested in Ecology as a scientific topic in 2002 with my field trip in Belize for my master thesis. There, I fall in love with the amazing environment of mangroves. But particularly, I felt as an ecologist during that time because I started to convert my natural curiosity into a scientific process of sampling and data analysis, dealing with plants interacting with and within their environment. During the many hours spent in Belizean mangroves, I liked imagining possible processes that drove the architectures of single trees or structure of the forest itself. I guess it is partly from these times as well that comes my interest for modeling and statistical tools trying to unraveling the hidden. I have been very influenced during this first experience by the own passion of Candy for the mangroves, as well as the inputs of Uta in imagining processes with her KiWi model. . . Once the master thesis was finished in 2003, I was lucky and happy to have the support of Uta and Professor Saint-Paul to get a position of PhD student in the MADAM project to develop a model on crab movements. However, you will see in the first part of the present thesis, that I did not focus only on crab ecology . . . My PhD became a continuation and improvements of what I had started in Belize on mangrove forest dynamic added to the new exciting topic of *Ucides cordatus* . . .

The jump into the PhD thesis might have been a bit fast, and the first experience of field work in Brazil was quite hard. But with the moral support of Martha, my Parents, Candy and Uta, I think I went through some very rich personal experiences and finally obtained interesting findings. . . At my return from Brazil, Uta and I proposed to have a new experience on the field few months later, this time a bit better prepared, and with a master student to investigate more on the movements of crabs based on the observations I had made during the first expedition. Before this second trip that was at the origin of most of the data on the spatial distribution of crabs, I learned C++ and developed the first versions of the IBU model. . . I was not convinced at first that IBU would bring important additional information. Volker was somehow the one that really believed in it more than myself, and finished to

convince me of the potential. . . The experience of trying to understand patterns with only hypotheses on some hidden processes was quite challenging and finally successful. Particularly now that I have done a second study with IBU (Chapter 8), I realize even more the potential for future theoretical, but also applied works.

From the development and trying to fit IBU to the field patterns was born the need of developing the approach of *POMIC*. This was actually another big experience and personal advancement. I had not much knowledge on likelihood methods or information criterion. However, few weeks after entering into this topic, appeared to me the possibility that one could estimate the likelihood of a non-linear stochastic model, which make *POMIC* interesting and paralleled to the famous Akaike information criterion. I have been very often doubting about the mathematical reliability of the “new method” created with it. After asking many specialists, I became quite convinced of its potential. And finally none of these specialists found that something was wrong in the *POMIC* approach. . . So I just have to hope now that it will be of help to other individual-based modelers. . .

In parallel of the *Ucides cordatus* and *POMIC* studies, I had also been working on the forest dynamic part and the KiWi model. I wrote and published my first paper (an important event in the life of an ecologist) with the big help of Candy and Uta during my first year of PhD. It is presented here because it fits particularly well with the other papers on mangrove forest dynamic, but the most important part (the field work) was done during my master. The origins of the work on simulating the influence of hurricanes on mangrove forest diversity were also coming from my master. However, in the paper presented here (Chapter 4), most of the work was done during the last three years. The last chapter of the first part on mangrove forest dynamic (Chapter 5) was then a connection between my new experience of tuning models (coming from the IBU model) and pattern-oriented modeling using the *POMIC* approach, so that it could be seen as parallel to the last chapter of the crab part.

Finally, the entire work I have done during 3 years (except the development of *POMIC*) was mostly turning around one special aspect: the observation and understanding of patterns hypothesized to be because of “competition”. . . Humans often believe that competition is one of the most important natural force at the base of any relationships, and particularly for their own ones. I would like not to believe in this direction, and I have always been quite attracted to the topic. I would have liked to try to demonstrate that competition-based relationships is not the solution for human populations. I am afraid my ecological work will never demonstrate that. . . At least not at all in this PhD thesis. But at last, I can comfort myself with the assessment

of the role of competition on other populations and communities. . . I have oriented the compilation of my articles to cover different aspects of competition and the expression of it under some few patterns. You will realize that I treated of inter and intra-specific competition in the two parts of the thesis respectively, and also discussed with the chapter 8 of asymmetric and symmetric competition. Even if far from being exhaustive, I covered interesting parts of competition situation in mangrove ecosystems. Finally, it leads me to a proposition of looking at competition with a probabilistic approach that I present in the conclusions chapter. Let see how this idea compete against other . . .

I want to finish this preface with an **acknowledgement part**. I would never have arrived to the present thesis without the help of many people. I will start with Uta Berger who supported me in all steps and advised me always frankly. I have also a big debt to Candy Feller with her transfer of passion for the mangroves and constant support on all the ecological parts of my work. Volker Grimm is then the third, but not less important, “mentor” that in particular convinced me that IBU works, I have to thank him at least for that. . . I am indebt to Professor Ulrich Saint-Paul, who made these three years possible. I would like also to thank Professor Julianne Filser for accepting to evaluate my work, and Heidemarie Wolter and Jonathan Montalvo to be on my defense committee.

There is a lot of people that helped me for some studies and that I would like to thank warmly: Karen Diele for the field work in Brazil and introduction to *Ucides cordatus*, Hanno Hildenbrandt for his talent on making C++ programming smarter, Marcelo Protazio for his explanations on geostatistics, Jonathan Montalvo for his mathematical advisory for the *POMIC* part, Marc Taylor and Gonzalo Olivares-Johnson for fruitful discussions on many ecological topics, Coralie D’Lima and Ulf Mehlig for the shared experience in Brazilian mangroves, Senhor Manuel, Domingos de Araujo and Aldo deMelo for the help in field work in Brazil, and Faustino Chi and the people of the Institute of Marine Studies for the work in Belize. Marc Taylor and Amanda Stern-Pirlot also helped me improving the English of parts of the thesis.

Even if they believe they are not so much involved in it, I think they do, and I would like to thank my parents for their constant love and support. To all the rest of my family and friends not yet mentioned I thank them also for supporting me in many ways. And finally, I have to confess that Martha Liliana Fontalvo Herazo made me happy and able to work on this PhD during all the three years. I am very grateful for her love and various way of help. She’ll continue to make me happy, allowing me to become father in some few months. . .

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Chapter 1

General introduction



This general introduction shall present general aspects of three main topics in my work: Ecological modeling, Competition and Mangrove ecosystems. In the first section, I present what ecological modeling is, what it may help to do and what are individual-based models and the pattern-oriented modeling approach. In the second section I explain what is generally understood under the concept of competition in ecology, present some examples of theories analyzing the role of inter- and intra-specific competition and arrive to what could be the role of individual-based models in these theories. In the third section, I present generalities of mangrove ecosystems and focus on two main components of Neotropical mangroves: (1) the tree community and particularly the three main species found in Caribbean mangrove forests; (2) the grazers community and particularly the leaf-removing crab *Ucides cordatus*. In the last section of this general introduction I present the general and methodological objectives of the thesis and the specific objectives of two parts of the thesis dealing each with a specific component of Neotropical mangroves. In this last section, I also present the temporal frame of my works, the fundings and the people involved in each following chapter.

1.1 The Whys and Hows of ecological modeling?

The science of ecology tries to understand interactions of living organisms among themselves and with their habitat (Haeckel 1866). Ecology, as many other sciences, combines two main approaches of analysis: observation and experimentation. The latter should identify the processes leading to patterns described by the first. Observations of natural systems should be accompanied of statistical, experimental and theoretical tools to avoid that ecology stays at the level of natural history. The descriptive part of ecology leads to many findings generally confirmed with experiments and thereafter accepted as general concepts. The plant succession concept (Cowles 1901) and the self-thinning rule (Yoda 1963) in plant ecology, or the predator-prey types of interactions (Volterra 1926, Lotka 1932 in Townsend et al. 2003) in animal ecology, are examples of largely accepted concepts developed after observations, mathematical descriptions and experimental tests at many scales. They are useful in the understanding of dynamics of resources of interest for humans, as well as generally in the understanding of natural systems.

However, many ecological concepts are debated. The problems might be first to describe the most holistically possible the natural patterns and second to understand all the phenomena behind them. The coupling of descriptive

and experimental ecology works at small level of integration (e.g. individual or population level) or small spatial or temporal scales but might not always at large scales. When the scale of integration is too large (e.g. at community or macroecological scale) or the spatial or temporal frame of the processes implicated is too wide, descriptive ecology can lead to interesting hypotheses but experimental ecology maybe less convincing or feasible. Such situations tend to happen for hypotheses originated after large scale observations. A good example of this is the intermediate disturbance hypothesis (“IDH”, Connell 1978). Obviously, the IDH could for example be experimentally tested on plankton (Flöder and Mosser 1999) or even bed mussels (Lenz et al. 2004). However, when speaking of systems with much larger regeneration time or spatial range (such as tropical forests), experiments are generally only partially reproducing the entire range of possibilities underlying the hypothesis. The IDH is therefore not yet accepted by all ecologists, and particularly those who focus on large scale questions (e.g. see argumentations on Mackey and Currie 2001, Sheil and Burslem 2003, Shea et al. 2004). The discussion around the IDH is one of many examples demonstrating the difficulties of experimentally assessing an hypothesis on large scale. In such cases, the “simulation part” of ecological modeling could enter into play and bring important inputs. I will define now what is meant by ecological modeling, and what is generally understood under the specific “simulation part”.

Ecological modeling could be defined as the creation of conceptual or mathematical models to synthesize acquired knowledge and illustrate or test hypotheses of the ecological science. This definition is very broad because we need to incorporate many different types of models: conceptual models (can be a diagram, some theoretical equations or even a specific formulation of a hypothesis), statistical models (generally developed to analyze data and test if these data support a focus hypothesis), flow models (describing the flow of energy or matter among compartments of a focus system assumed to be under steady state) and dynamic models. They are aiming at the same general objectives: combining previously acquired knowledge to go further on understanding. Dynamic models are generally focusing on the description of dynamics of population, species assemblage or community. They can have an additional aim not possible with the other ecological modeling approaches: the prediction of future trends in the focus system. Within these dynamic models, models using computer simulations constitute the “simulation part” of ecological modeling mentioned earlier. These models can be going from a simple equation describing just a population interacting with its environment, up to a model with structured description of different types of individuals in various populations of a community and describing their

intrinsic interactions as well as with the environment. The complexity of dynamic models depends on the purpose of the model and thereby the need of prediction power, the need of precision, the knowledge synthesized with the model, the problematic assessed in relation to this knowledge and the time allocated to the development of the model.

Grimm and Railsback (2005) argue that ecology and biology in general still lack strong mathematical tools to have the capacity to prove as logically as possible specific characteristics of natural systems. With the development of computer based models in the last 30-40 years, algorithm and mathematical approaches increased tremendously in complexity in response to the need of understanding of complexity of natural systems. Specifically, bottom-up dynamical modeling approaches have been developing a lot during the last 20 years based on the idea that a system is not just a sum of the parts. With these bottom-up models, ecologists organize and simulate the system of focus in compartments of identical level of integration to understand phenomenon at higher level of integration. In particular, the individual-based modeling (IBM, or also called agent-based modeling ABM) approach follows this framework and helped in understanding emergent properties of complex systems such as population or communities out of the characteristics, behavior and interactions of parts of this system, namely individual organisms (Breckling et al. 2005, DeAngelis and Mooij. 2005, Grimm et al. 2005).

Studies using individual-based modeling have increased linearly in the last 20 years with number of publications passing from 1 to 150 publications/yr between 1990 and 2004 (DeAngelis and Mooij, 2005). Some modelers believe that these tools could even become the fundamentals of a completely new approach to ecology and create their own theories (Grimm and Railsback, 2005). However, traditional ecologists call into question the reliability of these models because of their internal complexity, their lack of verifications against natural conditions, and the sometimes too high specificity of their results. These critics lead the IBM developers, and bottom-up modelers in general, to develop an additional approach named pattern-oriented modeling (POM). The objective of the POM strategy is to increase the reliability of the model and to use as overall development objective of an IBM the reproduction of some documented patterns of a system, described at different levels, and assuming they are the results of specific processes (Grimm et al. 1996, Wiegand et al. 2003, Grimm and Berger 2003, Grimm et al. 2005). The school of thought of POM does not generally use the term “emergent properties” to describe their patterns. This term is used often by another school of thought (e.g. Breckling et al. 2005). However, emergent prop-

erties are high level patterns ultimately. And when already described from field studies, these emergent properties should be a main focus of the POM strategy. The POM strategy has been described with a rigorous protocol including four steps (Wiegand et al. 2003): (1) “aggregation of individual-based biological information” for the model construction, (2) “determination of parameter values”, (3) “systematic comparison between the observed pattern and the simulated pattern produced by the model” and (4) “secondary predictions”. In the two last steps, systematic comparison of model results to field observations, either of focus (pattern, step 3) or non-intentional (part of the secondary predictions, step 4), should lead to the increase in reliability of the model that bottom-up modelers needed and were looking for with the POM approach. The two first steps assure the IBM or ABM to incorporate low-level information that is leading to the emergent properties or patterns at higher levels (e.g. behavior of individual fish forming a fish school when grouped, e.g. Reynolds 1987).

1.2 The competition concept in ecology

In ecology, the concept of competition comes from the concept of resource limitation that organisms face in natural situations. Both concepts of limitation of resources and competition were fundamental on the elaboration of ecological theories as early as for Darwin (1859) and his “struggle for life” concept. Limitation of resources is a major link between the organisms and their environment. Without such limitations, one could imagine that a population would grow toward an infinite size. Limitation of resources can happen mainly through two types of factors: abiotic (coming from the physical-chemical environment), or biotic. Competition enters into play as one of the major biotic responses to limited resources and may add further limitation pressure. As such, the competition concept integrates all types of interactions among organisms that limit in some way one or more resources to one or all organisms. This definition is close to the one Keddy (2001) proposes, and although he was far from being the first to give a definition (probably Clements et al. 1929), I will stick to his:

“Competition will be defined as the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability.”

This definition is disputable, but tries to integrate as many aspects as possible to be general enough but not too vague either. Specifically, this definition implies that:

- competition is an interaction;
- competition occurs primarily among individual organisms;
- competition leads to a negative effect on at least one of these organisms;
- competition is always for a resource (i.e. a resource ultimately mediates the interaction).

However, the definition intentionally leaves room for the multiple aspects of competition considered in ecology (all following descriptions according to Keddy 2001). The first aspect is the kind of resources to be considered. These resources can be anything necessary for the ecological success of the organisms in considerations: food, mates, nutrients, space, light, etc . . . They can be constant, seasonal or variable in time, spatially homogeneous or heterogeneous, multiple or unique, complementary or essential. The second aspect is the types of organism considered: if they are of identical species, we speak of intraspecific competition; if not we speak of interspecific competition. The third aspect is the mechanisms by which the negative effect occurs. It can be through direct interactions such as fighting, territorial behavior or poisoning. This is then defined as “interference competition”. Indirect competition happening through the use of common resources is defined as “exploitation competition”. The results of the effects are also considered to separate symmetric to asymmetric competition. The latter refers to a situation where an organism feels competition effects not varying proportionally to the sizes of the other competing organisms.

The description and the utility of the concept of competition was often discussed among ecologists (see e.g. Birch 1957, Harper 1961, Ekschmit and Breckling 1994). But keeping in mind the resource limitation definition, one can understand how important might be this type of interaction among organisms and its implication on ecosystems functioning. Keddy (2001) makes the parallel between competition as one of the fundamental forces connecting organisms to the gravitational force in the framework of Newtonian physics. He states that the three fundamental forces are competition, predation and mutualism. After analyzing the potential theoretical interactions among two organisms (or population) belonging to an identical ecosystem (Table 1.1), I would not simplify interaction forces among individuals as of only three kinds. However, looking at the resource-mediated interactions, one can realize the importance of the concept of competition. Apart from neutralism (theoretically rare for organisms belonging to the same ecosystem) and competition, all other cases of interacting organisms through common resources

are forming the group of so-called “positive interactions”. These are traditionally generalized to include commensalism, facilitation and mutualism and the last two are frequently indistinctly used as interchangeable. These positive interactions are under high interest by present ecologists (e.g. Kennedy and Sousa 2006, Bruno et al. in press).

One of the original and still most important question bringing interest to the way organisms interacts was the descriptions of so many different species and the question to understand why it is so (e.g. Hutchinson 1959). In this context, competition was of main focus for the development of evolution theory and speciation through natural selection proposed by Darwin (1859). More specifically, studying the processes of interspecific competition was thought very early to be fundamental for the objective of explaining species coexistence. Early theoretical works on these questions developed the Lotka-Volterra’s competition equations (Volterra 1926, Lotka 1932 in Townsend et al. 2003) and arrived to the “competitive exclusion principle”, also known as “Gause’s principle” (1934 in Tilman 1982). This principle states that when two competing species coexist in stable environment, they are in a situation of niche differentiation, and if this differentiation does not exist they are in a temporal non-equilibrium that will always end-up by the exclusion of one by the other. This principle was useful to understand and differentiate between the fundamental niche and the realized niche of a species (Townsend et al. 2003). However, the Gause’s principle has been revised a lot mainly because of many observations of species coexistence cases not according with it (Townsend et al. 2003). To cite only few theoretical works around these aspects, Levin (1970) for example focused on the temporal aspect and proposed to consider the lack of niche differentiation as periodic equilibrium situations. Tilman (1982) proposed a resource-based interspecific competition approach that for simple situations gave comparable results to the results of the Lotka-Volterra model, but then allowed also to differentiate the importance of spatial distribution of resources (e.g. Tilman 1994). The understanding that temporal and spatial variations in resources availability were important for explaining species coexistence in supposed interspecific competition situation oriented ecologists to look more at questions around how “resource partitioning” occur among competing species. This led Barot and Gignoux (2004) to even consider that “space and time are the ultimate resources” to consider in explaining plant species coexistence. In recent years, the concerns of space heterogeneity, temporal variability and resources-based approaches created a branch of ecology concerning non-equilibrium dynamics (e.g. Rohde 2005). Ultimately, non-equilibrium hypotheses and recent coexistence studies proposed that interspecific competition is much less important than originally believed in explaining the observation of high number

Table 1.1: Types of interactions among 2 organisms (or populations) (1 and 2) belonging to the same ecosystem. Defined according to the effect coming out of this relation for each organism (positive (+), negative (-) or no effect (=)) and depending on the mediator of the interaction: through one external resource (ER), many resources (MR) or because 1 is resource of 2 (1R)). Note that reproduction is not included because obviously not possible among every couple of organisms an ecosystem can present.

Effect on 1	Effect on 2	Mediator	Definition of interaction	Examples
+	+	ER or MR	Facilitation	Two plants creating a micro-climatic conditions (e.g. Callaway 1995)
+	+	1R	Mutualism or symbiosis	Cyanobacteria on corals (e.g. Rai et al. 2002)
-	+	MR	Competition for one resource and facilitation or commensalism on another (For ER impossible?)	Tree growing better with the nutrients fixed by understory plant although the latter could grow better without the shadow of the tree
-	+	1R	Predation, parasitism	Trophic interactions
=	+	ER or MR	Commensalism	Larvae using resources at different decay stages (Heard 1994)
=	+	1R	Commensalism	A tree (1) hosting a carnivorous species (2)
-	-	ER or MR	Competition	Trees in a forest, animals under limited resource conditions, etc ...
-	-	1R	Synnecrosis (rare)	Parasite killing its host before its reproduction
-	=	ER or MR	Total asymmetric competition (sometimes called Amensalism)	A tree (2) shading a seedling (1) that does not access the resources of the tree
=	=	ER or MR	Neutralism (rare)	
= or -	=	1R	Theoretically impossible	

of species in coexistence. At last, all these theories and many experimental studies arrived to differentiate between the potential of action of interspecific competition and its real importance (Townsend et al. 2003), which appear not to be the same.

Intraspecific competition was accepted in ecological concepts as early as the interspecific one. However, the focus questions were obviously different and not so fundamental. Very early, the role of intraspecific competition in populations' structures was integrated in theories of population biology. For example, the logistic growth models used in many fishery or population biology models assume intraspecific competition with the carrying capacity factor. Thereby, it is generally accepted that intraspecific competition explains the relationship among density and per capita available resource in some specific cases (Keddy 2001). For example, it is accepted to be at the origin of the self-thinning phenomenon observed in many plant and sessile organism populations. The self-thinning theory, or also called “-3/2 law”, assumes that the density of a population of approximately even-aged sessile organisms is related to the mean biomass of individuals with a constant power factor (α). It assumes also that this relationship is observable with dynamical follow up of a stand's growth ($Mean\ Biomass = Constant \times density^\alpha$, where $\alpha = -3/2$, Yoda 1963, see also reviews of Lonsdale 1990 or theoretical representation review of Reynolds and Ford 2005). Although the value of the power factor of the self-thinning relationship is discussed (e.g. Weller 1987), the competition for resource and particularly competition for space is widely accepted as main factor at the origin of this phenomenon. Relatively early (e.g. Klomp 1964) the competition for space was seen as a major part of intraspecific interactions. Doing so, space was seen as a resource, as it was lately accepted on the interspecific level. Intraspecific competition studies also analyzed the type of effect produced by competition: symmetric or asymmetric. A lot of studies theorized around the effect of these different types of competitions, particularly in plant systems, on the size distribution and growth patterns and ways of partition resources (e.g. see review Schwinning and Weiner 1998). Many studies focused on intraspecific competition to evaluate its relative importance against interspecific competition in population structures (many examples given in Keddy 2001, p21). This can be easily assessed when using the Lotka-Volterra competition equations and comparing the importance of the parameters related to inter- or intra-specific competition (see Townsend et al. 2003, p199). But ultimately, the acceptance of intraspecific competition was much less debated than for the role of interspecific competition in shaping communities. Many studies looked at the influence of intraspecific competition on size distribution patterns inside populations (e.g. in Klomp 1964). And intraspecific competition could

theoretically shape a population structure in general term of “coexistence of different stages organisms” as the interspecific competition was believed to influence communities. These differences of acceptance could come from the easy observations of organisms using common resources at similar life-stages. Additionally, the difference of resource-used or eventual resource partitioning between co-specific organisms of different life-stage are also common observations and thus can be more easily included in intraspecific theories than the resource partitioning questions at interspecific questions.

To caricaturize the situation of the concepts of inter- and intra- specific competition in ecology, I see the first as producing many theories that tried to be demonstrated by observations, while the second is based on observations leading to many theories. This relative contradictory situation could show that studies looking at the interspecific level often forgot the intrinsic importance of individuals and resources in the competition definition: competition (inter or intra) happen between individuals primarily, and resources are the vectors of any competition force. And particularly, the recent awareness of importance of space as an ultimate resource (Barot and Gignoux 2004) demonstrated the necessity of interspecific competition studies to come back at the individual-level. Assuming that the phenomena happening at the individual level are transmitted at higher integration level as emergent properties, interspecific competition theories should look further in this direction. These theories would learn probably more from the results of emergent properties coming from individual-level interactions and could be illustrated and compared with emergent properties of systems including only intraspecific competition. Already, some recent studies looked after species coexistence questions integrating the spatial and temporal aspects of resource partitioning at individual level to infer on community level patterns (e.g. Pachevsky et al. 2001). Additionally, several individual-based modeling studies looked at the implications of spatial competition on population structures (e.g. Pacala and Silander 1985, Weiner et al. 2001, Berger and Hildenbrandt 2003). The fast increase in bottom-up modeling capacities and simulation approaches should allow looking further in the coexistence questions with a process-based perspective.

1.3 Main components of Neotropical mangrove ecosystems

1.3.1 Generalities

“Mangroves” can refer either to the individual trees and shrubs growing in the intertidal zones of tropical and subtropical coastline creating tree assemblages, or to the assemblage of these trees itself (to avoid confusion, usually referred to as mangrove forest). A mangrove ecosystem is generally considered as an ecotone among the larger ecosystems that are open sea and terrestrial land. Mangrove ecosystems are therefore not really “closed” in term of fluxes of energy as the original ecosystem definition implies. It is generally accepted that a mangrove ecosystem includes: the organisms living in a tropical forested intertidal area (i.e. the mangrove forest area and adjacent waters), their interactions, the physical environment and the physical-chemical factors influencing these organisms. The distribution of mangrove ecosystems around the world is approximately between 30°N and 30°S. The southernmost extreme point of distribution is found in Australia at 38°45’S (Duke 1992), while the northernmost is in Bermuda at 32°20’ N (Saenger 2002). These distributions are correlated with the winter position of either the seawater temperature isotherm of 24°C (Barth 1982) or the isotherm of 16°C of air temperature (Chapman 1977), assumed as main factors limiting growth of mangrove trees in extreme areas. Mangrove ecosystems cover more than 10⁵ km² worldwide (Bunt 1992).

Two main biogeographical areas are differentiated: the Indo-West-Pacific hemisphere (IWP), and the Atlantic-East-Pacific hemisphere (AEP). Although the two hemispheres have almost equivalent spatial extent (Bunt 1992, Duke 1992), the mangrove tree species on IWP are much more numerous (40 to 58 species depending on authors) than the AEP ones (only 8 to 12 species). The Neotropical mangroves are more specifically referring to mangroves found on the American continents although they are approximately the same tree species than those found on western Africa.

Although the trees growing on intertidal areas have to cope with saline environment or tidal fluctuations of abiotic environment, on a global scale mangroves are among the most productive ecosystems on earth (Bunt 1992). However, many variations in term of productivity and ecosystem function have been noted. The geomorphological settings, inputs of nutrients and rainfall determine different types of productivity and functioning and thereby eventual transfer of organic matter to adjacent marine ecosystems (Jennerjahn and Ittekkot 2002). In term of primary production alone, some man-

grove areas are more productive than neighboring tropical forests (Saenger 2002). The primary production and standing biomass of the trees is the most important part of an extensive food web incorporating both marine and terrestrial organisms (Alongi 2002).

1.3.2 The “trees” component

Beside fixing nutrients and being at the base of the food web, mangrove trees also stabilize the sediments and provide physical habitats presenting several micro-systems: canopy, trunk and non-inundated aerial roots, intertidal root system, below ground roots. Each micro-system has an associated community of primary and secondary consumers relatively distinct from the one of other micro-system. Mangrove trees are usually found on sheltered areas, away from strong wave actions although they might also be capable of reducing wave energy (Mazda et al. 1997 in Saenger 2002). The forests they constitute can be of many different forms that can be classified according to their physiographic and structural attributes (described by Lugo and Snedacker 1974: overwash, fringe, riverine, basin, hummock and dwarf), their physical-chemical environment (soils types, tidal range, etc . . .), their geomorphological settings (river-dominated, tide-dominated, barriers, lagoon, alluvial plains, etc . . .) or their phytosociology (describing the group of species encountered) (see Saenger 2002). These needs of classifications and the actual diversity of forms illustrate the high plasticity and physiological capacities of the few mangrove tree species (see Ball 1988).

Mangrove forests are highly dynamic, presenting many different adaptations to specific situations. The concept of forest dynamics includes all the processes related to the life history of individual trees and the evolution of the tree assemblage through time. An example of dynamical concept can be the species dominance succession. It was at first believed to be linked to a land building capacity of mangroves (Davis 1940). The species succession and land-building concepts were intensively discussed (e.g. Lugo 1980, Johnstone 1983) and particularly in relation to the observation of species zonation patterns. It appears now that land-building does not seem to be a specificity of mangrove forests, and not at the origin of species zonation patterns (Smith 1992). The species succession concept was then often attributed to changes in abiotic conditions (Tomlinson 1986), and rarely linked to interspecific competition (see Ball 1980, Berger et al. 2006).

For the Caribbean mangroves, the three main species (*Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*) have different capacities to deal with stresses (McKee 1995c). Chen and Twilley (1998) included these characteristics in an individual-based simulation model, reproduced observa-

tions of basal area of Florida, and obtained species dominance succession occurring over 500yrs. However, these simulations assumed phases of large proportion of trees of identical species dying together because of identical ages (what is generally named senescence of a stand). Duke (2001) adapted a theoretical model (Jiménez et al. 1985, Fromard et al. 1998) to analyze mangrove forest dynamics as a whole (irrelevant of the place), including the gap dynamic concept. The results of this model hypothesize that senescence phases would rarely happen in mangrove forests, in accordance to many observations (Duke 2001) but theoretically in contrast to the model of Chen and Twilley (1998). But finally, Fromard et al. (2004) documented senescing phases to occur at large scale on the coast of French Guyana, mainly driven by erosion, and re-adapted the theoretical model to include large scale geomorphological phenomena.

These differences of theories of dynamics observed by different mangrove ecologists could be seen as different dynamical pathways that mangrove forests can take in general and in the Neotropical mangroves in particular. These pathways might be dependent on frequency of large scale disturbances (erosion or hurricanes), small scale disturbances (gap formation) and growth conditions (nutrient, temperature and light conditions are for example more favorable in Brazil or French Guyana compared to Florida for the same set of species). These growth conditions could then be the main factors supporting or not strong interspecific competition leading to the observation of succession at fast (less than decade, as in Berger et al. 2006) or slow speed (more than century, as in Chen and Twilley 1998).

1.3.3 The “grazers” component

Trophic modeling studies showed that the main part of the primary production in Neotropical mangrove ecosystems is either largely consumed by primary consumers organisms (e.g. Wolff et al. 2000) or exported offshore to neighboring ecosystems (e.g. Vega-Cendejas and Arreguín-Sánchez 2001). The consumption pathway is generally assumed as driven by large benthic communities of crabs or snails (e.g. Wolff et al. 2000, Proffit and Devlin 2005). Direct grazing on the trees by crabs (e.g. *Aratus pisonii*, Beaver et al. 1979) or insects (e.g. Feller 1995, Feller and Matthis 1997, Feller and McKee 1999, Saur et al. 1999) were also observed and could be of importance on the flows of energy in Neotropical mangroves. Another pathway is the decomposition of leaf-litter primary production through bacteria (Alongi 2002). All these pathways of fate of trees' biomass are influencing the retention or recycling characteristic of mangroves, and thereby the general role of these ecosystems.

In Neotropical mangroves, the main primary consumers of benthic community influencing the energy pathways seems to be either the semi-terrestrial crab *Ucides cordatus*, shown as of particularly high ecological importance in North Brazil (Wolff et al. 2000, Koch and Wolff, 2002, Schories et al. 2003, Nordhaus et al. 2006), Equator (Twilley et al. 1997) and the Dominican Republic (Geraldes and Calventi 1983) or eventually a snail species *Melampus coffeus* as in Florida (Proffit and Devlin 2005). These two potentially high primary consumers are showing a much lower species richness than the benthic grazers community of sesarimid crabs found in the IWP biogeographic area (e.g. Skov and Hartnoll 2002). This might be explained by the lower tree species richness and thereby lower diversity of food sources in the Neotropics.

The biology of *Ucides cordatus* (Linnaeus 1763, or *Ucides cordatus cordatus* on the Atlantic side and *Ucides cordatus occidentalis* on the Pacific side) was recently studied in more details. Twilley et al (1997) for Ecuador and Nordhaus et al. (2006) for Brazil demonstrated with the role of this species the original misbelief that Neotropical mangroves had leaf-litter processing pathways based on detritus while the IWP ones were based on grazing by decapod crabs (McIvor and Smith 1995). For Brazil in particular, many studies of the MADAM project (Berger et al. 1999) illustrated its important economical role (Glaser and Diele 2004), its key role in ecosystem structure (Wolff et al. 2000, Koch and Wolff 2002) and ecosystem function (Schories et al. 2003, Nordhaus et al. 2006). *Ucides cordatus* is a slow growing species (Diele et al. 2005) feeding preferentially on *Rhizophora mangle* leaves falling from the trees (Nordhaus 2004), and does not seem to have direct competitors for this resource within the benthic community (Koch and Wolff 2002). It creates deep burrows on the sediment where it stays inside most of its time, or stand close-by outside waiting for leaves to fall (Nordhaus 2004). This crab population appears to be food limited on the Caeté Peninsula (Nordhaus 2004), a 140km² mangrove peninsula, focus area of the MADAM project. Intraspecific competition, at least interference competition, is believed to happen from behavioral and feeding strategies observations (Nordhaus 2004). This population is subject to a high fishing pressure, hypothesized at first to be leading to over-fishing situation (Wolff et al. 2000), but later observed as relatively stable and anyway far from threatening biological sustainability (Diele et al. 2005). This is mainly due to the traditional fishing techniques of the crab collectors of this area and the main interest of the market for large males much older than sexual maturity (Diele et al. 2005). Another interesting aspect of the fishing techniques is the possibility to distinguish in the favorite fishing grounds that are the *Rhizophora mangle* forests, fishing areas where the crab collectors can access and pull the crabs out of their burrows, and non-fished areas that crab collectors cannot access because of too

high root densities (Diele et al. 2005). These situations were hypothesized as producing buffer systems also avoiding entire depletion of large male stocks in *Rhizophora mangle* forests (Diele 2000).

1.4 Objectives and presentation of the thesis

1.4.1 General and methodological objectives

The general context of the present thesis is to investigate the importance of competition as a factor structuring ecological communities and populations. More specifically, I expect that competition for space at the individual level could shape spatial and eventually temporal patterns of community and population structure. Considering that inter- and intra- specific competition could be both analyzed from an individual-based perspective, I am interested in possible parallels between the two roles of spatial competition in structuring respectively communities and populations.

I selected for this purpose two systems, one at each level: (1) the Caribbean mangrove tree community to study interspecific competition and (2) the North Brazilian population of the mangrove crab *Ucides cordatus* to analyze the role of intraspecific competition. Two different parts corresponding to these two systems under analysis are treated with a group of 3 articles each (Chapters 3 to 5 and 6 to 8 respectively, see Fig. 1.1). The first article of each part presents a field study on spatial patterns of interest for each system: one at community level (looking at the spatial distribution of species) and one at population level (looking at the spatial distribution of individuals). The following two articles of each part analyze with the help of individual-based models (see Fig. 1.1) the role of competition, and specifically spatial competition, for the reproduction of the spatial patterns and the observation (or reproduction) of temporal patterns (see Fig. 1.1 for chapters using the pattern-oriented modeling approach). The general objective can be summarized as:

Study with the help of individual-based modeling the importance of competition among individuals for the spatial organization of two major components of Neotropical mangroves.

Each part has nevertheless specific objectives in relation to the ecology of the focus systems. These specific objectives are in parallel since entering under the general objective. A general discussion and conclusion (Chapter 9) comes back to these specific and general objectives and looks at possible parallels

between interspecific and intraspecific competition roles in the respective shaping of communities and populations.

As said above, I apply the pattern-oriented modeling approach for most individual-based modeling studies. On this methodological aspect, the present thesis has also the objective:

Develop, evaluate and use a criterion based on information theory for the evaluation of models in quality of pattern reproduction.

The motivations of development and the “pattern-oriented modeling information criterion” (*POMIC*) are presented in Chapter 2. It is used in Chapters 6 and 8, and indirectly compared to other methods in Chapter 8 (see Fig. 1.1).

1.4.2 Specific objectives

Part I. Interspecific competition in Caribbean mangrove forests.

The Caribbean mangroves are of particular interest for studying interspecific competition since these communities show only three to four true-species of mangrove trees. This obviously would not help on answering the general question “why so many species?” seen above, but the factors allowing or not local coexistence of these three species could be seen as easier to investigate at individual level than if the system would comprise several tens of species. Caribbean mangroves are additionally frequently disturbed by large scale disturbances such as hurricanes and tropical storms, which make the study of secondary recovery dynamic possible and of importance. Patterns of zonation and succession of species dominance were observed (e.g. McKee 1995a,b , Ball 1980), hypothesizing that interspecific competition for space might be a major factor on structuring these tree communities. Additionally, with the same set of species, data from Fromard et al. (1998) showed that the self-thinning dynamic was observable, which is relatively rare for tropical forests (Saenger 2002). Thus, competition for space is happening among individuals of these species.

Another advantage in studying this group of tree species is that two individual-based models are already parameterized for them: FORMAN (Chen and Twilley 1998), and KiWi (Berger and Hildenbrandt 2000). The KiWi model, a spatially-explicit individual-based model, was developed during the MADAM project (Berger and Hildenbrandt 2000). This model has the characteristic of simulating competition for space among individuals at the individual level (while at the gap level in Chen and Twilley’s). Thus,

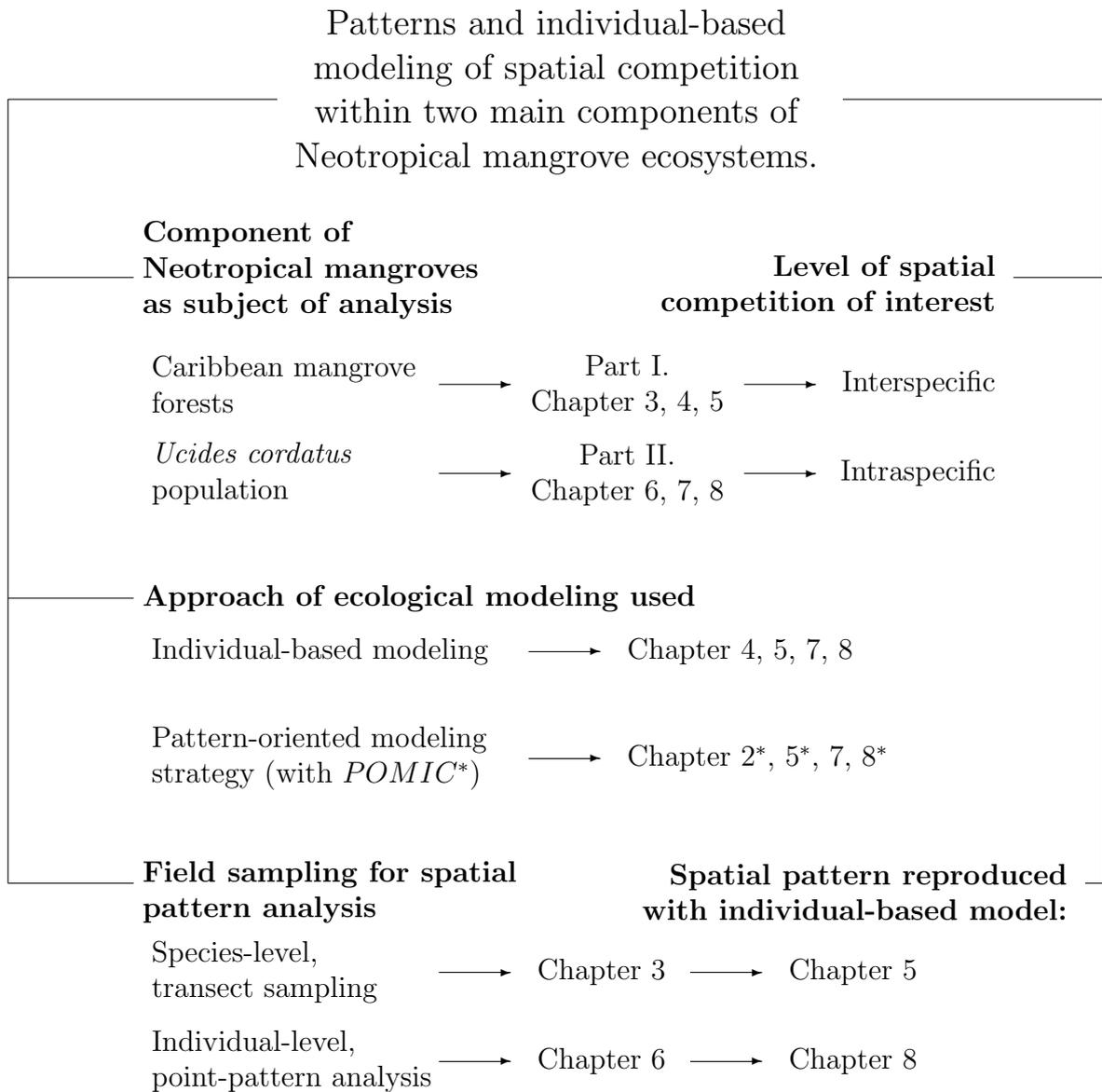


Figure 1.1: Presentation of the general topics and methods covered by the different articles (referenced by Chapter numbers) of the present thesis.

the KiWi model is a perfect tool for the study of influence of interspecific spatial competition at the individual level on the production of spatial and temporal patterns.

I focus in this part on the typical spatial pattern of species zonation, and analyze the temporal pattern of succession under the general question of the intermediate disturbance hypothesis (Fig 1.2). These succession and zonation patterns are patterns of mangrove tree species coexistence in a given intertidal area. The specific objective of this part can be summarized as to:

Study the importance of abiotic factors and interspecific spatial competition happening at individual-level as processes explaining succession and zonation patterns in Caribbean mangrove forests.

In this part, Chapter 3 ¹ focuses on documenting 4 patterns of zonation around a Belizean offshore mangrove island, Calabash Cay, and investigate the possible role of a large scale disturbance on the heterogeneity of species dominance of zones within the zonation patterns of the 4 sites. Thereby, I try to analyze factors explaining the coexistence of species in some zones while other zones are mono-specific. Chapter 4 analyzes deeper with the KiWi model the possible factors influencing species diversity (in term of heterogeneity of dominance) in Caribbean mangrove stands. Chapter 4 also looks at the factors influencing species succession and the implication of succession in observing intermediate disturbance hypothesis pattern (Connell 1978). Chapter 5 investigates the specific role of abiotic factors on the zonation patterns described in Chapter 3, assuming that interspecific competition for space occurs at individual level.

Part II. Intraspecific competition in North Brazilian *Ucides cordatus* populations

The situation of *Ucides cordatus*, as the only invertebrate species using leaf-litter falling from the trees in the benthic community of North-Brazilian mangroves (Koch and Wolff 2002), makes it a perfect model species to analyze intraspecific competition effects on population structure without having to consider also interspecific competition. Results of the MADAM project studies on the mangroves of the Caeté peninsula provides much information on *U. cordatus* population structure, life-cycle (Wessels 1999, Diele 2000,

¹Note that the field work and analyses of this Chapter were done during my MSc. studies

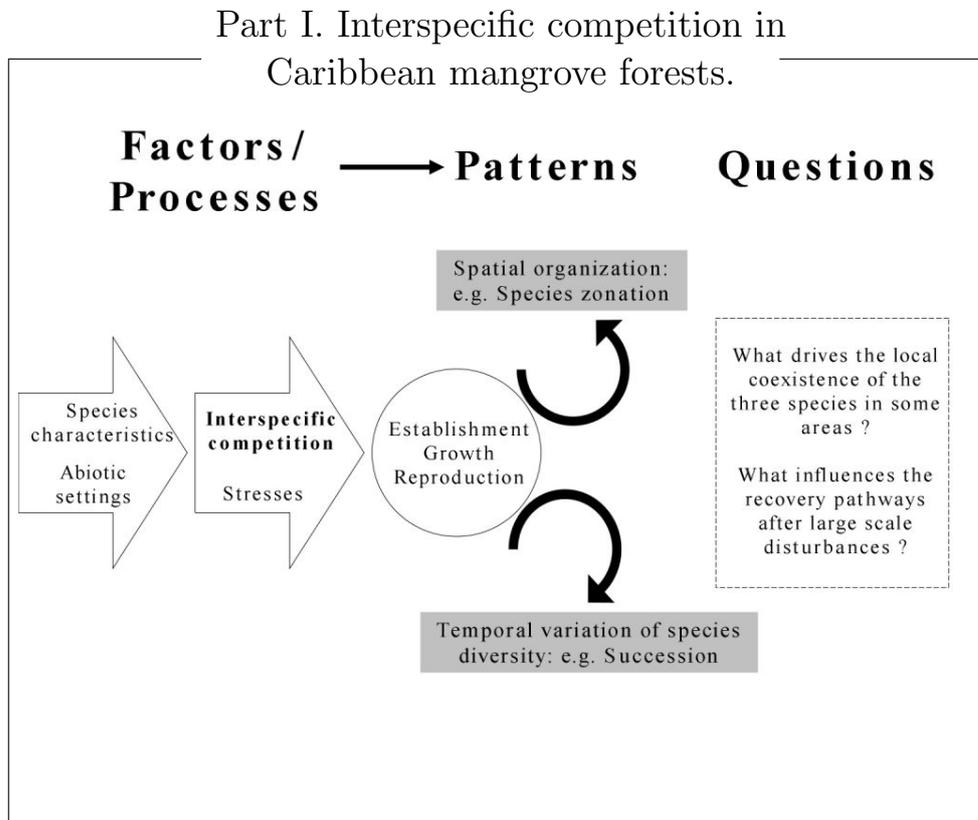


Figure 1.2: Theoretical framework of the objectives of the first part of the present thesis: “Study the importance of abiotic factors and interspecific spatial competition happening at individual-level as processes explaining succession and zonation patterns in Caribbean mangrove forests”. Note that the Questions are part of the theoretical framework as direction of investigation, not as question to be entirely answered.

Diele et al. 2005), behavior (Nordhaus 2004, Nordhaus et al. 2006), and ecological role (Wolff et al. 2000, Koch and Wolf 2002, Schories et al. 2003). It was observed as having a spatial distribution varying in size and density according to habitat types (Wessels 1999, Diele 2000, Nordhaus 2004). Dynamical aspects of population structure are particularly interesting to study to understand how fished areas are recolonized by individual crabs when these areas have been harvested by humans. Crab collectors reported relatively constant recolonization time (personal communications, Diele). The

buffer mechanisms proposed by previous studies (Diele 2000), might be at the origin of this temporal pattern of recovery which was however not analyzed thoroughly so far (only a small experiment in Diele 2000). The spatially structured population and the recovery of harvested areas are indicators that individual crabs change burrows. Thus, studying the movements of the crabs would give interesting inputs for the processes at the origins of the hypothesized spatial or temporal patterns.

Intraspecific interference competition was observed to happen among individuals either for burrows or for food (Nordhaus 2004). Exploitation competition for *Rhizophora mangle* leaves was less evident but also possible since the crabs appeared to be food limited (Nordhaus 2004). Both interference and exploitation competition in this species could be considered together as competition for space by the individuals. I focus on the second part of the present thesis on studying the impact of this intraspecific competition on the movements of *U. cordatus*, and thereby its spatial distribution and recovery patterns (Fig. 1.3). The specific objective of this part is to:

Study the importance of intraspecific spatial competition among individuals as process explaining recovery and spatial distribution patterns in North Brazilian *Ucides cordatus* populations.

In this part, Chapter 6 aims at documenting the spatial patterns of distributions of individuals within *R. mangle* dominated and *Laguncularia racemosa* dominated forests. It looks at the individuals' spatial distribution on small (<10m) and large scale (>10m) and potential abiotic and biotic factors influencing the latter. An individual-based model is presented in Chapter 7: the Individual-Based *Ucides* or IBU. It was developed with the pattern-oriented modeling approach focusing on two patterns of recovery after small scale fishery documented also in Chapter 7. The aim of this chapter was to analyze the role of intraspecific competition in the decision of crabs to leave their burrows. Chapter 8 uses also the IBU model. It focus on analyzing the role of asymmetric competition and distance of resources competed for on the behavior of crabs leading to the spatial pattern at small scale observed on Chapter 8 and the recovery patterns of Chapter 7.

1.4.3 Administrative presentation of the thesis

Different parts of the present thesis were written as articles since October 2003. Thereby, the thesis is a cumulative document of 7 articles (Chapter 2 to 8) integrated with a general introduction (the present chapter) and a general discussion and conclusion (Chapter 9). The Chapter 3 field work and analysis was done during my ISATEC master thesis (University of Bremen),

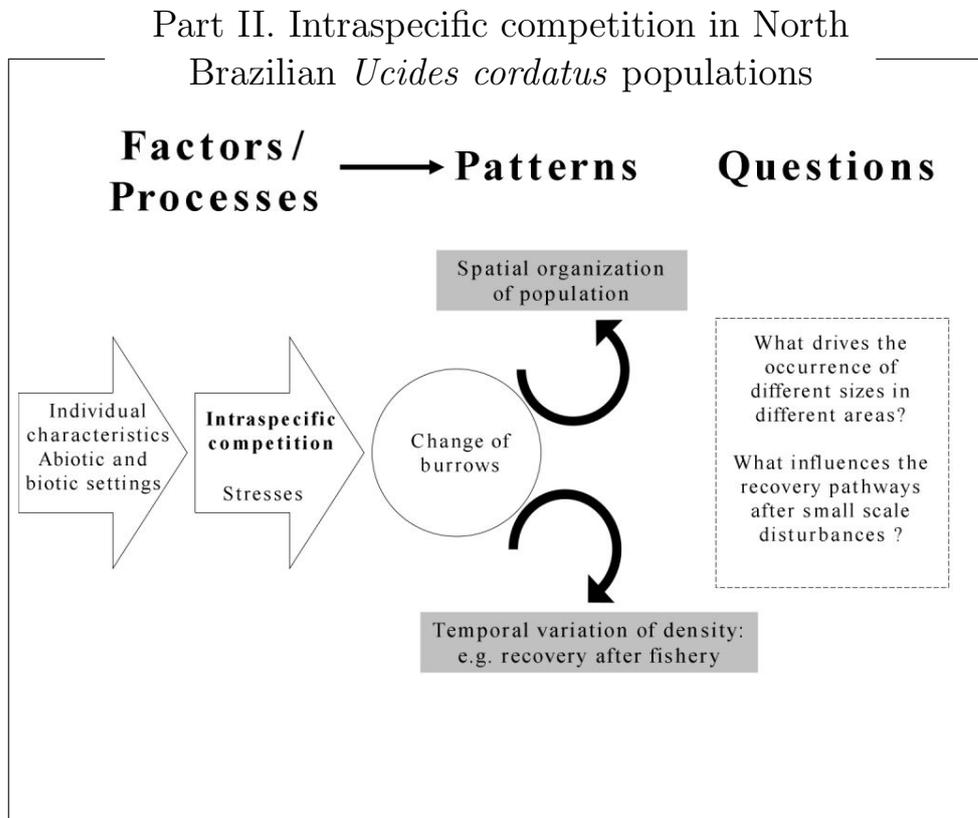


Figure 1.3: Theoretical framework of the objectives of the second part of the present thesis: “Study the importance of intraspecific spatial competition among individuals as process explaining recovery and spatial distribution patterns in North Brazilian *Ucides cordatus* populations”. Note that the Questions are part of the theoretical framework as direction of investigation, not as question to be entirely answered.

but the article presented here was reworked during the last 3 years and I believed it was necessary to include it here as field background of the first part.

All the works would not have been possible without the help of many people (see Preface) and particularly the co-authors of the 7 articles. I describe in Table 1.2 the respective participations of each co-author, the title of each article, its corresponding chapter number and funding source according to the main years of work. In addition to the described responsibilities in Table

1.2, all co-authors participated in elaboration of concepts and discussions on ideas of the respective works.

The main funding of this thesis was the MADAM project (MAngrove Dynamics And Management), a bilateral cooperation between the Center for Tropical Marine Ecology (ZMT) at the University of Bremen, Germany and the Federal University of Pará (UFPA) in Belém, Brazil, and financed by the Brazilian National Research Council (CNPq) and the German Ministry for Education and Research (BMBF) under the code 03F0154A, which supported me and my field work from the 1st of October 2003 to the 31st of December 2005. The PUME (PUffer MEchanismus) project was granted to Dr. Uta Berger by the DFG under the code BE 1960/2-1, for financing my position and theoretical works from the 1st of January 2006 to the 31st of December 2006. The ZMT financed directly computers and other material facilities, and 4 additional months for my position.

Table 1.2: Titles of the articles constituting the present thesis with corresponding Chapter number, a brief description of the involvements of each co-authors and the main funding sources and year of work corresponding (PUME was a DFG project (BE 1960/2-1), MADAM was a CNPq-BMBF project (03F0154A), and the NSF fundings were granted to I.C. Feller for the field work and sample analyzes (DEB-9981535).)

Article title	Chapter	Descriptions of responsibilities	Fundings (year)
Proposing an information criterion for individual based model selection	2	I developed the POMIC and wrote the manuscript. Uta Berger participated in the idea's development and for the writing	PUME (2006)
Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane	3	I did the field work, the analysis and the main part of the writing. Candy Feller participated in field work development and in the writing. Uta Berger participated in the writing. Faustino Chi helped for the field work.	NSF (2002-2004)
Modeling the effect of hurricane disturbances on mangrove forest diversity	4	I did the simulations, the analysis and the main part of the writing. Uta Berger participated in the analysis and writing. Hanno Hildenbrandt helped in the simulation and developed the idea presented in Appendix A. Candy Feller participated in the writing.	MADAM (2003-2005)
Importance of abiotic gradients on mangrove zonation patterns: a simulation experiment	5	I did the simulations, analysis and the main part of the writing. Uta Berger participated in the writing. Candy Feller participated in the idea's development.	MADAM & PUME (2005-2006)
Spatial structure of a leaf-removing crab population in a mangrove of North-Brazil	6	I did the field work, the analysis and the main part of the writing. Uta Berger and Candy Feller participated in the writing.	MADAM (2003-2005)
Simulating cryptic movements of a mangrove crab: recovery phenomena after small scale fishery	7	I developed the model, did the simulations, the analysis and the main part of the writing. Uta Berger and Volker Grimm participated in the analysis and writing. Karen Diele participated in the writing. Hanno Hildenbrandt helped for the development of the model. Coralie D'Lima did a part of the field work.	MADAM (2003-2006)
Testing intraspecific phenomenological competition models at individual-level to reproduce population-level patterns of a mangrove crab	8	I did the simulations, the analysis and the writing.	PUME (2006)

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Chapter 2

Proposing an information criterion for individual based model selection



Proposing an information criterion for individual based model selection

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Parts of this chapter will be submitted as an article with an identical title

2.1 Abstract

Agent-Based and Individual-Based Models (ABM/IBMs) have been improved in quality and reliability in recent years with an approach called pattern-oriented modeling (POM). The POM proposes guidelines to develop models trying to reproduce patterns observed on the field and test systematically how well the ABM/IBMs reproduce them. POM studies used generally traditional methods of goodness of fit such as the sum of squares evaluation or “hand made” comparisons of fitting errors and variations.

Model selection is also a new statistical approach in ecology that assesses more than two hypotheses at the time against a set of field data. The tools used for this purpose are usually information criterion such as the Akaike’s Information Criterion (AIC). These are based on information theory and help doing inference in a multimodel context.

Although both approaches focus on the explanation of patterns by evaluating the potential underlying processes, the link between the information criteria and the POM was so far never done. This study proposes an information criterion for model selection in a POM context (the pattern-oriented modeling information criterion: *POMIC*) using similar principles than the AIC. We describe how to calculate *POMIC* for different types and numbers of patterns to be fitted. We present derived statistics that can be calculated with *POMIC* and help in doing strong inference from a set of ABM/IBMs, or allow calculating likelihood maximized parameter values in a context of inverse modeling. We illustrate the use of *POMIC* with a simple example of application. We discuss the precautions and advantages of *POMIC*, and conclude that the use of the *POMIC* gives to POM a new potential of inference on the understanding of “behaviors” of individual part of complex adaptive systems.

Key Words: agent-based and individual-based modeling, pattern-

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oriented modeling, information theory, Akaike’s information criterion.

2.2 Introduction

The use in social sciences and ecology of agent and individual-based models (ABM/IBMs) started about 20 years ago and increased quickly with the development of computation capacities (Grimm 1999). The general critics of the first IBMs were to be either too theoretical or too simple to be reliable in the application to concrete problems, or to be too complex and unreliable in case of necessary generalizations to wider horizons. The pattern-oriented modeling (POM) approach was then developed to counter-balance these critics by developing and testing IBM with the objective to reproduce patterns observed in nature (Grimm et al. 1996, Railsback, 2001, Brang et al. 2002, Wiegand et al. 2003, Grimm et al. 2005). The first purpose of POM was to develop, scale and parameterize IBMs according to the reproduction of natural patterns (e.g. Wiegand et al. 1998). The methods of reducing parameter uncertainty and selection of best parameter sets can be called “inverse modeling” (Grimm et al. 2005) to refer to the identical methods used in other modeling exercise (e.g. statistical or linear modeling). A second purpose of the POM approach, together with one of the original ones of individual-based modeling was to test different hypothesis of processes at an individual level against natural patterns observed at higher integration level. This was called by Grimm et al. (2005) the “strong inference” procedure. This second part of POM could be paralleled to the model selection procedures using different statistical models and information criteria to create a context of multimodel inference.

Multimodel inference (or “model selection” depending on authors) is used more and more often in natural sciences (review by Johnson and Omland, 2004). Its principle is to confront several working hypothesis at a time against a set of data. In this procedure, one should formulate different verbal hypotheses first, express them mathematically, give a goodness of fit indicator to each statistical model and end up doing inference in either strongly selecting one hypothesis or keeping a set of plausible ones with different weights. Thus, this approach’s philosophy is to conclude about a set of most likely phenomena influencing focus data, although sometimes it could arrive to select the most likely one. Multimodel inference contrasts with the classical method of testing a null hypothesis to accept or reject the alternative hypothesis of interest. Generally to make the inference, the approach uses information criteria to rank the statistical models fitting empirical data. In particular

the Akaike's information criterion (AIC) and its derivative (Akaike 1973, 1974, Bozdogan 1987) considering both goodness of fit and statistical model complexity are the preferred criteria. The AIC was developed to extend the likelihood ratio test approach to multimodel situations adding an increasing bias for more complex models fit with a maximum likelihood estimator:

$$AIC(k) = -2 \log \left(L \left(\hat{\theta}_k \right) \right) + 2k \quad (2.1)$$

where k is the number of parameters in the model, \log is a natural logarithm function, and $L \left(\hat{\theta}_k \right)$ is the likelihood of the parameters' maximum likelihood estimates of the statistical model given the data to be fit. The rationale is to penalize overparameterization with the $+2k$ part and find a compromising well fitting and as parsimonious as possible model. This information criterion and its derivative have been used widely in model selection and elaboration in many other sciences (e.g. geophysics: Hipel 1981, pharmaceuticals: Yamaoka et al. 1978). In natural sciences it is particularly used in the comparison of non-nested models in mark-recapture studies (e.g. Huggins 1991, Lebreton et al. 1992, Anderson et al. 1994, Caswell et al. 1999, Yoccoz et al. 2001, Langtimm and Beck 2003) and model selection of DNA sequence evolution (e.g. Posada 2001, 2003). It has also been used in different cases of statistical models selection of dispersion (e.g. Doncaster et al. 1997) and selection of different types of autoregressive models of population variations (e.g. Hansen et al. 1999, Post et al. 2002).

Despite the similarity of purpose of multimodel inference and POM, there is still a lack of equivalent tools to the AIC for the pattern-oriented approach for IBMs. The expression of a likelihood function to iterate deterministically the values of parameters of complex simulation models limited the approach. Particularly, parameters linked to individual behaviors implemented in a complex IBM are almost impossible to estimate with such functions considering patterns observed at a higher integration level as data to be fit (e.g. population spatial distribution patterns emerging from the behavior and interactions of individuals). Therefore, likelihood estimator functions were rarely developed for non-linear models such as individual based or other types of bottom-up rule-based models. In only one case testing a simple dispersion IBM, Mooj and DeAngelis (2003) used likelihood functions to find the parameters' maximum likelihood estimate describing individual behavior, but in this case fitting patterns also at individual level. Without maximized likelihood estimates for the parameters used in a model, the assumptions of the AIC and derived information criteria do not stand. We need consequently to think about how to apply the principles of the AIC approach so useful in traditional multimodel inference so that IBMs developed for the analysis and understanding of emergent properties appearing in complex adaptive

systems can be analyzed with the strategy of the model selection procedure. So far, some studies used statistical tools such as deviation methods for the parameterization phase of individual-based models (e.g. Wiegand et al. 1998, 2003, 2004 Kramer-Schadt et al. 2004), and arrived to very coherent results. However, to the best of our knowledge the second phase of model selection and inference from them has generally been done by qualitative criteria (e.g. Berger et al. 2006), rarely with mathematical tools (e.g. Wiegand et al. 2004), and never with indicators of goodness of fit based on information theory.

The objectives of this study is to propose a pattern-oriented modeling information criterion (*POMIC*) for inverse modeling and/or strong inference applied to ABM/IBMs in order to understand a complex adaptive system by reproduction of multiple patterns. Although our main focus is on IBMs in ecology, this criterion would apply for any bottom-up rule-based model developed within a POM context. We first present the tools already existing and used in POM studies for inverse modeling and inference on multiple models to illustrate the need of an information theoretic based approach. Secondly, we explain the main information theoretic principle of the AIC to propose adaptations and new assumptions for the *POMIC* in order to have it based on similar principle. Then we recommend derived statistics that can be extrapolated from the use of AIC to the use of *POMIC* for strong inference and for inverse modeling parameterization. An example of application is presented with a simple case of IBM developed to understand the individual behavior behind emergent properties of a simple system. Finally, we discuss the advantages of *POMIC* on the other indicators of goodness of fit and its general potential for future pattern-oriented modeling studies.

2.3 Actual tools of pattern-oriented modeling

In the original definition of pattern-oriented modeling (Grimm et al. 1996), the patterns of focus were considered as information coming from natural systems that underlined a hypothesis of process. However, the patterns used in the pattern-oriented modeling approach since then were generalized to any kind of information not directly includable in the model parameters coming from field observations and the underlying hypothesis aspect was somehow put to a second importance. In this context, Wiegand et al. (2003) proposed a pattern-oriented modeling protocol which follows 4 steps: (1) “aggregation of individual-based biological information” for the model construction, (2)

“determination of parameter values”, (3) “systematic comparison between the observed pattern and the simulated pattern produced by the model” and (4) “secondary predictions”. The third step includes what could be paralleled to an “inverse modeling” phase, although the focus patterns in this protocol might be individual-level behavior as well as higher-level patterns. From the way Wiegand et al. described the secondary predictions, some might also be called emergent properties (e.g. Breckling et al. 2005) or population-level patterns. Thus, the “strong inference” on individual behavior proposed with different models leading to these population-level patterns is a part of this protocol’s fourth step. In both the inverse modeling part and the strong inference part of the pattern-oriented modeling approach, an important aspect is to estimate how well the models fit the field observations. Different tools exist to do so.

The first simple analyses are visual assessments by selecting the best model from the different graphical output of simulations compared to the field observations. Grimm (2002) proposed to call this type of assessment the visual debugging procedure. At the beginning of model development, it can be as simple as trying freely different parameterizations and algorithms and observe the results coherence. In further analysis, the parameter selection should follow some coherent criteria and the results should also be analyzed more thoroughly and can lead to graphs or table showing their proximity to field observations. This is used a lot with individual based or grid-based models in ecology (e.g. Jeltsch et al. 1997, Thulke et al. 1999, Railsback and Harvey 2002, Groeneveld et al. 2002, Eisinger et al. 2005, Berger et al. 2006). Visual debugging is particularly useful for preliminary analysis and building phases of a simulation model. However, these methods are subject to the modeler decision and lack of precision for a systematic comparison to select among a parameterization set, or to do inference on hypotheses proposed by different models.

For the “inverse modeling” step, Wiegand et al. (2003) proposed to use deviation methods to estimate how far each parameterization is from the field patterns. Let a pattern be defined by the observations $i = 1, 2 \dots n$ in the space \mathfrak{R} , the corresponding empirical measurements $X = x_1, x_2 \dots x_n$, and the simulation results of one replicate done with a process-based model be defined by $Y = y_1, y_2 \dots y_n$. The deviation (d) is calculated for each measurement by:

$$d_i = x_i - y_i \tag{2.2}$$

The mean squared deviation (*MSD*) is one of the criteria derived from the

deviation:

$$MSD = \frac{1}{n} \sum_{i=1}^n (x_i - y_i)^2 \quad (2.3)$$

Kobayashi and Us Salam (2000) decomposed the *MSD* in several components linked to the correlation analysis parameters, allowing verifying where is the major part of the deviation of a simulation results coming from. Gauch et al. (2003) proposed another decomposition to solve the problems of links among the components of Kobayashi and Salam and allow a better comparison of models as to know which part is the least robust to reproduce the empirical data. However, all these considerations were usually not taken into account by IBM developers, using most of the time the root mean squared deviation (*RMSD*) as a criterion (e.g. Jamieson et al. 1998, Wiegand et al. 1998, 2004, Kramer-Schadt et al. 2004, Chapter 6) to work with the actual distance between the simulation results and the empirical measurements:

$$RMSD = \sqrt{\frac{1}{n} \sum_{i=1}^n (x_i - y_i)^2} \quad (2.4)$$

These techniques allow an estimation of the deviance of the simulation results to the focus pattern. The objective is to minimize this deviance when processing a fine tuning of a model (e.g. Wiegand et al. 1998). When considering m replicates of a simulation model, the objective is to minimize the sum or the mean of these deviances as indicators of the error of the model (e.g. Wiegand et al. 2004). However, this way does not consider the variance of the error among replicates. A solution is to try to minimize both the error expressed by these indicators and the variance (e.g. Chapter 6).

In general, the use of the deviation methods is combined with a threshold criteria coming from assumptions (e.g. Wiegand et al. 1998) or randomization of field data (e.g. Wiegand et al. 2004) to evaluate if the simulation results are acceptable. This leads to binary results as to accept or not a parameterization for its capacity to reproduce field patterns. Other statistics than a deviation method can lead to these binary results. The comparisons among the field data ranges of variation and simulation results range might be one. Statistically, this could be done for example with a Wilcoxon signed ranked test (as in Higgins et al. 2001). Using any binary criteria, the best parameterizations would be the ones with all patterns reproduced. For the “strong inference” part it is possible to generalize these binary criteria to select the best models as the ones reproducing all patterns. However, at this level, the quantitative goodness of fit of one good model compared to another is not kept, and the strong inference is then only qualitative even

if several models contradict each others. In such case, estimating relative scores obtained for the different patterns allow attributing a global score to each model but the variance is harder to introduce. And when dealing with different type of pattern such as combination of temporal series and spatial distribution, this scoring analysis are even getting more complex because dealing with different measurement types and units. A likelihood measure instead of a distance measure would help solving these problems.

Drechsler (2000) introduced the concept of likelihood for selection of model parameterizations with a simple approach based also on the ranking of simulation results. However, he did not consider different complexity of models and the likelihood estimates where not based on information theories. Mooij and DeAngelis (2003) did apply an information-theory-based likelihood calculation on the estimation and reliability estimation of parameters of three models of different complexity. But their patterns of focus were at individual level, i.e. at the same level than their parameters. An adaptation of the AIC approach using likelihood for the assessment at all level of goodness of fit was then believed to allow these comparisons of models fit to several patterns and considering for each of them the error and the variance of error of the simulation results. The interesting aspect of this adaptation would also be to be able to use the same approach for the inverse modeling and strong inference part.

2.4 An information criterion for pattern-oriented modeling

2.4.1 Background

One of the main principles of the AIC development (Bozdogan 1987) is to minimize the Kullback-Leibler information divergence between the “truth” and the model in consideration. The Kullback-Leibler information divergence (I) is assessed between the true distribution described by a probability function $f(x)$ of a variable of focus x and the predicted distribution described by a probability function $g(x)$ of a statistical model describing the variations of x so that:

$$\begin{aligned} I(f(x); g(x)) &= \int_{-\infty}^{+\infty} f(x) \log \frac{f(x)}{g(x)} dx & (2.5) \\ &= \int_{-\infty}^{+\infty} f(x) \log f(x) dx - \int_{-\infty}^{+\infty} f(x) \log g(x) dx \end{aligned}$$

This function is considered as loss function of doing statistical modeling in the AIC development (see Bozdogan 1987, Burnham and Anderson 2002). Akaike suggested the use of $2 \times I(f(x); g(x))$ as an estimator of the quality of a statistical model which parameters were previously estimated with a maximum likelihood estimator (i.e. an equation returning the most likely value of the parameter given the data to be fit). Since further assumptions of the AIC are based on the assumption to use a maximum likelihood estimator for the parameters, we need to reconsider the approach and cannot apply directly the AIC to rule-based models.

Statistical models consider a possible parameter set θ influencing the focus variable. AIC assumed that this set of parameters was part of the set of parameters θ^* influencing the true distribution of the focus variable x . Focusing on bottom-up rule-based models, not only parameters might have an influence on x but also processes. This terminological difference implies that we compare models with different algorithms corresponding to different hypotheses of processes or individual behavior in the special case of IBMs, and not obviously with different numbers or values of parameters. An advantage of this approach is that the sampling processes (Z) influencing the sample outcome can be considered. By incorporating the sampling processes in a rule-based model, a comparison of model outcomes and field sample can be done with at least one known common underlying influencing process. This can be compared to the “virtual ecologist” procedure used in different IBM studies (e.g. Berger et al. 1999, Wiegand et al. 2003). In our opinion, the pattern-oriented modeling approach should always consider this point so that data produced by models are really comparable to field patterns. Assuming that the effect of sampling is the same on model outcomes and sample distribution, we can now compare the predicted distribution of the model described by a probability function $g(x|\theta)$ (where θ are the processes simulated in the rule-based model) with the sampling distribution described by a probability function $b(x|\theta^*)$ (where θ^* are all the processes that influenced the outcome of the sampled variable), with both θ^* and θ including Z . The latter probability function would be taken as an indicator of the hypothetical true probability distribution function $f(x|\theta^{**})$ (where θ^{**} are all the processes influencing the true distribution), which is not assessable otherwise in any kind of modeling (statistical or bottom-up) since the processes or parameters behind the data are assumed unknown from the beginning and have to be analyzed by the procedure. The Kullback-Leibler information divergence between the sampling probability distribution and the rule-based model outcome distribution can then be used as a loss function of our rule-

based pattern-oriented modeling approach. The equation 2.5 will become:

$$\begin{aligned} I(b(x|\theta^*); g(x|\theta)) &= \int_{-\infty}^{+\infty} b(x|\theta^*) \log b(x|\theta^*) dx - \int_{-\infty}^{+\infty} b(x|\theta^*) \log g(x|\theta) dx \\ &= -H(b(x|\theta^*); b(x|\theta^*)) + H(b(x|\theta^*); g(x|\theta)) \end{aligned} \quad (2.6)$$

The first part of the right hand side of equation 2.6 is the negative Shannon entropy of the sample probability distribution $-H(b(x|\theta^*); b(x|\theta^*)) = -H(b(x|\theta^*))$ and is constant. Thus, comparing several models, the one showing the lowest cross-entropy $H(b(x|\theta^*); g(x|\theta))$ will have the lowest information divergence. Once estimated the two probability functions $b(x|\theta^*)$ and $g(x|\theta)$, we could then use the cross-entropy as an indicator of goodness of fit of the model to the focus pattern.

2.4.2 Proposition

Let assume an individual-based stochastic model developed to reproduce the n observations of the continuous variable x over \mathfrak{R} , with corresponding empirical measurements $X = x_1, x_2 \cdots x_n$. The simulation results of one replicate of the model with identical sampling process (with identical number of observations) are $Y = y_1, y_2 \cdots y_n$. A function ($b(x)$) giving the probability of observation of x can be assumed (Appendix A - page 53) and considered as estimate of $b(x|\theta^*)$ so that:

$$\begin{aligned} b(x|\theta^*) &> 0 && \text{for any } x \in X \\ b(x|\theta^*) &= 0 && \text{for any } x \in]-\infty; X_{min}[\text{ or }]X_{max}; +\infty[\\ \text{and } \sum_{i=1}^n b(x_i|\theta^*) &= 1 \end{aligned}$$

where X_{min} and X_{max} are the minimum and maximum observed field values of x respectively. A probability function $g(y)$ (or an estimator of it) should be fit to the simulations results Y so that it is defined over \mathfrak{R} , and can then estimate $g(x|\theta)$. We describe in Appendix A (page 53) how to estimate these probability functions, and in Appendix B (page 56) the special case of $n = 1$.

We propose, out of equation 2.6 (see Appendix C - page 56 for mathematical argumentation) an estimator of goodness of fit of Y to X , the pattern-oriented modeling information criterion (*POMIC*) with the following formula:

$$POMIC = -\frac{1}{n} \sum_{i=1}^n b(x_i|\theta^*) \log(g(x_i|\theta)) \quad (2.7)$$

This *POMIC* value should go towards 0 as $g(x|\theta)$ is getting toward $b(x|\theta^*)$, i.e. Y is close to be X . If the range of the values of $g(x|\theta) > 0$ incorporate the range $[X_{min}; X_{max}]$ then *POMIC* is a numerical value $< \infty$. If the range $[X_{min}; X_{max}]$ does not incorporate $g(x|\theta) = 0$ then for some $x \in [X_{min}; X_{max}]$, and *POMIC* could be assumed to be infinite.

With S replicates of the model analysis, the distribution should be estimated for each replicate s so that each will have a particular estimator of $g(x|\theta) \equiv g_s(x|\theta)$. The goodness of fit of the model could then be calculated with:

$$POMIC = -\frac{1}{n} \sum_{i=1}^n \left[b(x_i|\theta^*) \frac{1}{S} \sum_{s=1}^S \log(g_s(x_i|\theta)) \right] \quad (2.8)$$

In this case, the larger S is, the more precise the estimation of the goodness of fit would be.

In the special case that the pattern of consideration is given by only one observation of one variable $x_{\text{unique obs}}$, we could assume that $b(x_{\text{unique obs}}|\theta^*) = 1$ and therefore the *POMIC* would be given by:

$$POMIC = -\log(g_{\text{All } s}(x_{\text{unique obs}}|\theta)) \quad (2.9)$$

where $g_{\text{All } s}$ is a probability function fit to the results of the unique observation of S replicates of the IBM (see Appendix B - page 56).

In the case of a study with several models developed to reproduce multiple patterns, after the assessment of goodness of fit of single patterns, the strong inference on the models fitting all patterns might need a criterion including the goodness of fit of all patterns together. Considering φ patterns p (of equal importance), each of these p pattern described by ϖ_p different independent variables, with for each variable $n_{p,j}$ observations, the *POMIC* would be:

$$POMIC = -\frac{1}{\varphi} \sum_{p=1}^{\varphi} \left(\frac{1}{\varpi_p} \sum_{j=1}^{\varpi_p} \left(\frac{1}{n_{p,j}} \sum_{i=1}^{n_{p,j}} \left[b_{p,j}(x_i|\theta^*) \frac{1}{S} \sum_{s=1}^S \log(g_{p,j,s}(x_i|\theta)) \right] \right) \right) \quad (2.10)$$

The *POMIC* is an estimator of the Kullback-Leibler divergence between the model and the sample distribution patterns. The statistics used in traditional model selection procedures with the AIC can then be applied as well to the *POMIC* (the following are derived from Burnham and Anderson, 2002).

2.4.3 Derived statistics for strong inference

The first statistic derived from an information criterion is the differences of fit. Since the *POMIC*, as the AIC, does not have real units and could

range widely, interpreting a *POMIC* value makes only sense by comparing it to other *POMIC* values of models fit to the same samples. Thus we can use the differences Δ_i as for AIC:

$$\Delta_i = POMIC_i - POMIC_{min} \quad (2.11)$$

where $POMIC_{min}$ is the smallest *POMIC* value of the model set R . The Δ_i can be interpreted as “strength of evidence” (Burnham and Anderson, 2002) where the best model will have $\Delta_i = 0$, and the other have $\Delta_i > 0$. Following the rules of thumb of Burnham and Anderson (2002) we can propose the following for different models:

- with $\Delta_i \leq 1$, the models have substantial evidence,
- with $2 \leq \Delta_i \leq 4$, the models have considerably less evidence,
- with $\Delta_i > 5$, the models have essentially no evidence.

The second use is the relative likelihood of each model given the data and the set of models tested (R). This can be calculated from the *POMIC* differences as:

$$L(model_i|data, R) = \exp(-\Delta_i) \quad (2.12)$$

From this relative likelihood estimator, pairs of models j and h can be compared with an evidence ratio ER :

$$\begin{aligned} ER &= L(model_j|data, R) / L(model_h|data, R) \\ &= \exp(-\Delta_j) / \exp(-\Delta_h) \\ &= \exp(POMIC_h - POMIC_j) \end{aligned} \quad (2.13)$$

which inform about the relative evidence of model h to model j .

The most important and handy part is the equivalent to the Akaike weights, w_i that normalize the model likelihoods such that they sum to 1:

$$w_i = \frac{\exp(-\Delta_i)}{\sum_{r=1}^R \exp(-\Delta_r)} \quad (2.14)$$

These give weights of evidence in favor of each model i and can be seen as the probability that it is the best model among the set R of models tested. So, if the best model w_i is so that $w_i > 0.9$ we could say that with 90% confidence this is the best model we have to reproduce the processes that influenced the variable x so that we observed the pattern given by the data. In other cases, strong inference would be done by understanding which models could be reproducing the processes that drove the observed patterns, and which other are unlikely to have been.

2.4.4 Derived statistics for inverse modeling

Another important use of Akaike weights is for model averaging. Model averaging for the case of individual-based models in a pattern-oriented modeling approach would come back to considering the inverse modeling part of POM, i.e. find the best fitting parameter values. Let assume one model structure including the processes θ with one unknown parameter k . Testing several values of k against the sample data producing the patterns of interest would then gives a set R' of different models just with different parameterizations. The POMIC and derived Akaike weights could be calculated as described earlier. If the best fitting parameterization is not one of the extreme tested values of k , then one could average the values to find a maximized likelihood estimate of $k \equiv \hat{k}$ as follows (from Burnham and Anderson, 2002):

$$\hat{k} = \sum_{i=1}^{R'} w_i \times k_i \quad (2.15)$$

With a variance given by:

$$\hat{var}(\hat{k}) = \left[\sum_{i=1}^{R'} w_i \left[var(k)_i + (k_i - \hat{k})^2 \right]^{1/2} \right]^2 \quad (2.16)$$

where $var(k)_i$ would be a potential variance of the parameter k a priori implemented in the model i .

Ideally, this approach could even be effectuated to multiple parameters situations. This sequence of inverse modeling could enhance a lot the POM approach if applied for the different type of models with different underlying hypothesis of processes before a sequence of strong inference on them.

2.5 Example of Application

For this example of application we propose to consider a theoretical experiment that could be conducted on individuals of an imaginary species in an enclosed square area of 100 by 100m. These individuals would have two possible statuses: active or inactive. From the biology of these individuals we would not know how the active individuals actually move or interact with their neighbors, but we would know that the inactive status would be for 4 days. Leaving randomly distributed 25 individuals at the beginning of the experiment we would observe during 50 days that the proportion of moving individuals would always be 0.5 standard deviation of 0.1. After these 50

days, the spatial organization analyzed with the L-ripley function (Besag on Ripley 1977) would show a significant regular distance between the individuals of 10m (Fig. 2.1). An individual based model could be constructed with the POM approach to reproduce these two patterns of proportion of moving individuals and regular organization after 50 days. We first describe a simple model to analyze this situation: the SIMOVIM (Simple MOVement Individual Model). Secondly, we describe the application of the *POMIC* for an inverse modeling analysis. And finally, we show how to use *POMIC* for a strong inference procedure.

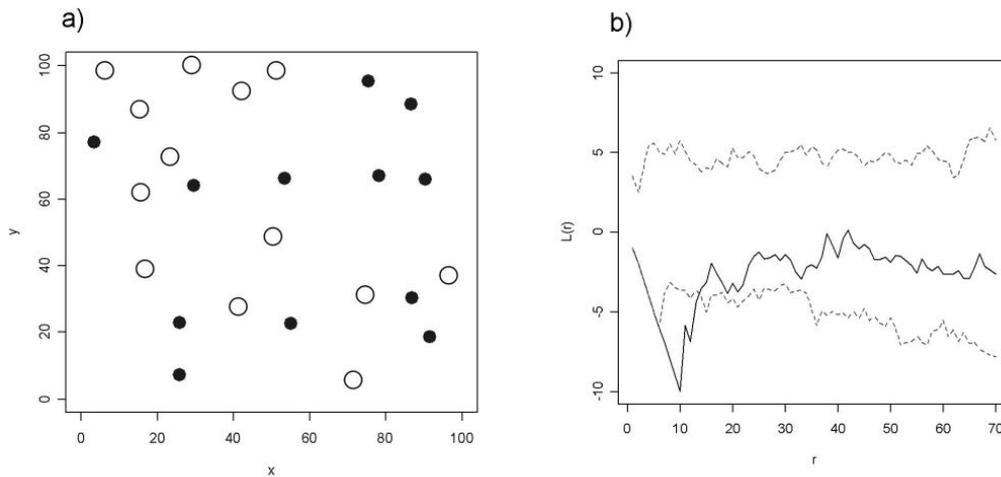


Figure 2.1: Spatial distribution of theoretical individuals after 50 days in their enclosure. a) individuals represented with respective x and y axis of positions and 2 statuses of active/inactive (black/empty respectively). b) L-Ripley analysis (Besag on Ripley 1977) where the black line is the L function of the map a) and the dashed lines are confidence envelope created with 999 Monte-Carlo randomization of the 25 individuals' positions.

2.5.1 Description of a simple individual movement model (SIMOVIM)

In this part we describe the SIMOVIM model following the ODD protocol (Grimm et al, 2006). First we give an overview description (purpose, state variables and processes), then we present the design concepts and finally the details (initialization, input, sub-models).

The purpose of the SIMOVIM model was to test hypothesis of movement of individuals leading to a regular distribution after 50 time steps. The state variables describing the individuals were the position and the statuses

(active-inactive) allowing the individual to move or not. The simulation area was a square of 100 by 100 m with reflective boundaries. The status of each individual was checked at each time step, and eventually changed according to two probabilities ($P_1 = 0.25$ and P_2 , Table 2.1) from one to the other status (inactive to active and active to inactive respectively). Active individuals were then moved with a given function of movement depending on the sub-model in use (random movement, attracted movement, repulsed movement, attracted and repulsed movement).

The SIMOVIM model reproduced an emergent property of spatial organization depending on the sub-model of movement in use. The proportion of individuals moving per day (hereafter referred to as PM) was also tested against the assumed pattern of observation described earlier (a fixed series $PMobs$ of 50 normally distributed random numbers of mean 0.5 and standard deviation of 0.1), but was obviously forced by the ratio P_1/P_2 . In all except the first movement sub-models, the individuals sensed their neighbors in the selection of its closest one. The change of status was stochastically determined. Each time steps, the frequency of movement and proportion of inactive individuals were recorded. The spatial organization was only assessed after 50 time steps. At initialization, the individuals were placed randomly on the simulated area and their status randomly assigned with a ratio of 1:1 for inactive/active individuals. No input was attributed to the model after this initialization. The first sub-model of movement was simulating a random walk (SIMOVIM version 1). The new position of the individual was assigned with the following formula:

$$\begin{pmatrix} x \\ y \end{pmatrix}_{t+1} = \begin{pmatrix} x \\ y \end{pmatrix}_t + \begin{pmatrix} rand_1 \\ rand_2 \end{pmatrix} \quad (2.17)$$

where $rand_1$ and $rand_2$ were two uniform random number between $-MaxMovD$ and $+MaxMovD$ (Table 2.1). The second sub-model simulated attraction of individuals until a given threshold (SIMOVIM version 2). For each individual, first the closest neighbor was found and if its distance ($Dist$) was above $MaxNeighD$ (Table 2.1), the new position was given as:

$$\begin{pmatrix} x \\ y \end{pmatrix}_{Focus\ t+1} = \begin{pmatrix} x \\ y \end{pmatrix}_{Focus\ t} + \begin{pmatrix} (x_{closest} - x_{Focus}) \times \frac{MaxMovD}{Dist} \\ (y_{closest} - y_{Focus}) \times \frac{MaxMovD}{Dist} \end{pmatrix} \quad (2.18)$$

where $x_{closest}$ and $y_{closest}$ were the coordinates of the closest neighbor. If the distance $Dist$ was below $MaxNeighD$ the focus individual made a random movement as in (2.17). The third sub-model simulated repulsion between individuals until a given threshold (SIMOVIM version 3). For each individual, the closest neighbor was found and if its distance ($Dist$) was below

Table 2.1: Tested values of the parameters included in the different versions of the SIMOVIM models.

Model versions (sub-models)	Parameter of probability to change status P_2 <i>active to inactive</i>	Maximum distance of movement in one direction ($MaxMovD$)	Threshold of interaction with the closest neighbor ($MaxNeighD$)
1	0.05 to 0.5	0.5 to 20	-
2	0.05 to 0.5	0.5 to 20	2 to 25
3	0.05 to 0.5	0.5 to 20	2 to 25
4	0.05 to 0.5	0.5 to 20	2 to 25

$MaxNeighD$ the new position was given as:

$$\begin{pmatrix} x \\ y \end{pmatrix}_{Focus\ t+1} = \begin{pmatrix} x \\ y \end{pmatrix}_{Focus\ t} + \begin{pmatrix} (x_{Focus} - x_{closest}) \times \frac{MaxMovD}{Dist} \\ (y_{Focus} - y_{closest}) \times \frac{MaxMovD}{Dist} \end{pmatrix} \quad (2.19)$$

If the distance $Dist$ was above $MaxNeighD$, the focus individual was set to make a random movement as in (2.17). The fourth sub-model simulated both repulsion and attraction, using the two equations (2.18) and (2.19) in cases of distance with the closest neighbor above and below the $MaxNeighD$ respectively (SIMOVIM version 4).

2.5.2 Using POMIC for inverse modeling parameterization

Methods

The parameters presented in table 2.1 were assumed unknown for the biology of our theoretical individuals. The first pattern to be reproduced was the proportion of individuals moving per day (PM). This was not possibly influenced by the $MaxMovD$ and $MaxNeighD$ parameters in SIMOVIM. We therefore tested 20 different values of P_2 with 1000 replicates of SIMOVIM

with the first movement sub-model and a fix $MaxMovD = 10$. For each replicate j we considered the observation of PM of each day to reproduce a vector of 50 observations $PMsim_j = PMsim_{j,1}, PMsim_{j,2} \cdots PMsim_{j,50}$, so that a probability function of appearance of PM values was created for each replicate ($g_j(PM|P_2)$) out of a histogram of this $PMsim_j$ vector. For each observation t of $PMobs$, we calculated the probability $b(PMobs_t|sample)$ to have observed the $PMobs_t$ value from the sample. We then applied equation 2.8 to calculate the $POMIC$ values for each parameter P_2 :

$$POMIC = -\frac{1}{50} \sum_{t=1}^{50} \left[b(PMobs_t|sample) \times \frac{1}{1000} \sum_{j=1}^{1000} \log(g_j(PMobs_t|P_2)) \right] \quad (2.20)$$

We calculated the Δ_i and w_i values out of the 20 $POMIC$ values with equations 2.11 and 2.14 respectively. A maximum likelihood estimate and variance of P_2 was then computed following equations 2.15 and 2.16. The second pattern to be reproduced was the spatial organization analyzed with the L-Ripley function. Each model version was tested with 100 replicates of each parameterization possibilities (Table 2.1) and with $P_2 = 0.25$. We assumed that the 70 $L_{obs}(r)$ values along the r axis of the pattern measurement were independent variables with each a specific probability distribution. Thus, for each r we used the 100 replicate results to construct a probability function $g_r(L(r)|model)$ to evaluate the probability to reproduce the $L_{obs}(r)$ value. We applied for each r value the equation 2.9 and summed them to obtain the overall $POMIC$ value:

$$POMIC = -\frac{1}{70} \sum_{r=1}^{70} \log(g_r(L_{obs}(r)|MaxMovD, MaxNeighD, sub - model)) \quad (2.21)$$

We then calculated the Δ_i and w_i values for each movement sub-model with equations 2.11 and 2.14 respectively. The maximum likelihood estimates and variance of $MaxMovD$ and $MaxNeighD$ were computed following equations 2.15 and 2.16. In both cases the $g(x|model)$ functions were created with a density kernel estimator of the R software (R Development Core Team ©2006) applied to the considered vector X of simulation results and scaled to fit an histogram of probability of occurrence.

Results

The $POMIC$ values varied between 1.5 and 0.3 for the different values of P_2 . The best fitting parameter (i.e. the smaller $POMIC$ value) was

found with $P_2 = 0.2$, but the weights calculation showed that no case had a probability > 0.07 to be the correct parameter value (Appendix D, Table 2.3). The averaging of P_2 with the weights of evidence gave an estimate of $P_2_{MLE} = 0.234 \pm 0.11$. This range of variation include the expected value of $P_2 = P_1 = 0.25$ so that the original 50% proportion of active individuals of start stay over the 50 days. The averaging is however not leading exactly to this expected value because of the small number of observations per replicates ($n = 50$).

For the first SIMOVIM version, with the sub-model of random walk, the different tested values of $MaxMovD$ showed infinite values of $POMIC$ (Appendix D, page 59). This meant that no parameterization case fitted correctly the spatial organization pattern, which was expectable since the movement was spatially random. For the second SIMOVIM version, with the sub-model of attraction walk, all the combination of tested values of $MaxMovD$ and $MaxNeighD$ showed infinite values of $POMIC$ (Appendix D, page 59). This meant that no parameterization fitted correctly the spatial organization pattern.

For the third SIMOVIM version, with the sub-model of repulsion walk, the best parameterization was found with a $POMIC = 1.166$, $MaxMovD = 2$ and $MaxNeighD = 10$ (Appendix D, page 60). The averaging of $MaxMovD$ and $MaxNeighD$ with the weights of evidence gave estimates of $MaxMovD_{MLE} = 4.88 \pm 3.27$ and $MaxNeighD_{MLE} = 10.14 \pm 1.59$.

For the fourth SIMOVIM version, with the submodel of repulsion and attraction walk, the best parameterization was found with a $POMIC = 1.426$, $MaxMovD = 6$ and $MaxNeighD = 15$ (Appendix D, page 60). The averaging of $MaxMovD$ and $MaxNeighD$ with the weights of evidence gave estimates of $MaxMovD_{MLE} = 7.42 \pm 1.79$ and $MaxNeighD_{MLE} = 18.16 \pm 1.85$.

2.5.3 Using POMIC for strong inference on individual behavior

Methods

The different SIMOVIM versions were now known as to reproduce the second pattern of spatial distribution or not. We used only the third and fourth version for this example of strong inference since the two first one were known not to reproduce the field pattern of spatial distribution. However, to effectuate a real study with strong inference, we should be testing a wider set of potential models reproducing relatively well the field patterns.

We run 100 replicates of each SIMOVIM versions (3 or 4) with stochastic

values of P_2 , $MaxMovD$ and $MaxNeighD$ around the averages found in the previous part and with their respective standard deviation ($P_2_{MLE} = 0.234 \pm 0.11$; for version 3: $MaxMovD_{MLE} = 4.88 \pm 3.27$ and $MaxNeighD_{MLE} = 10.14 \pm 1.59$; for version 4: $MaxMovD_{MLE} = 7.42 \pm 1.79$ and $MaxNeighD_{MLE} = 18.16 \pm 1.85$). The overall POMIC for the fit of the two patterns were then calculated as:

$$POMIC = \left(-\frac{1}{50} \sum_{t=1}^{50} \left[b(PMobs_t|sample) \frac{1}{1000} \sum_{j=1}^{1000} \log(g_j(PMobs_t|P_2)) \right] - \frac{1}{70} \sum_{r=1}^{70} \log(g_r(L_{obs}(r)|sub - model)) \right) / 2 \quad (2.22)$$

We calculated the Δ_i and w_i values for the 2 movement sub-models with equations 2.11 and 2.14 respectively.

Results-Conclusions

The SIMOVIM versions 3 and 4 with the best fitted parameters lead to $POMIC$ values of 0.956 and 0.996 respectively. The differences among them being so small (< 0.1), the weights of evidence were 0.52 and 0.48 respectively. This indicated that the version 3 of SIMOVIM with the sub-model of repulsion walk and the version 4 with the sub-model of repulsion and attraction walk were almost identically likely to be reproducing the behavior of our theoretical individuals.

However, the strong inference out of this exercise was that the repulsion is surely happening to arrive at the reproduction of the considered patterns. The model versions without repulsion did not reproduce the spatial distribution pattern. The addition of attraction to the repulsion process did not enhance the fit, nor did it decrease it substantially. Thus, it could not be discarded as a biological process happening in addition to repulsion. But following an Ockham's Razor principle of using the least complex model for an equivalent payoff as to reproduce reality (defined as the Medawar Zone by Grimm et al. 2005), the use of the version 4 instead of version 3 would be superfluous if one wants to work on further aspect of this population with the SIMOVIM model.

2.6 Discussion

We described and applied a new tool adapted from information theory for evaluating the goodness of fit of stochastic rule-based models for which a deterministic equation of maximum likelihood estimates of the parameters

can not be computed. This condition particularly applies to agent-based and individual-based models that are trying to reproduce field observations at higher integration level. We have proposed also a set of derived statistics to estimate evidence weights and maximized likelihood estimates of parameters that were demonstrated in our example to be useful for strong inference and inverse modeling respectively.

About the parsimony of models assessed by POMIC

The reasoning of checking over-parameterization of statistical models with AIC and of ABM/IBMs with *POMIC* have identical objectives: increase the model's predictability (or payoff) with increase complexity until this complexity increase does not increase payoff. Considering a statistical model including random and/or non-random parameters, their number might increase fit capacity but might also lead to an increase of variability that at some given point does not favor the overall fit. Model selection criteria such as AIC (actually often replaced by more complex one), use an over-parameterization penalization including the number of parameters in the formula. These criteria can then indicate easily if it is worth to increase the number of random/non-random parameters or not. In the POM context, the objective being the same, the interest was to determine at which point the fit increase is not worth the increase of complexity. We demonstrated with our SIMOVIM example that using the *POMIC* allows, with an information theoretic basis, to do such conclusions. The number of parameters or processes is not in *POMIC* but because it is an estimate of a Kullback-Leibler (K-L) distance as the AIC, the goodness of fit differences and weight of evidences allow us to discard or not a more complex model applying the famous Ockham's Razzor. Consequently, the fact that the number of parameters or processes of the model assessed with *POMIC* does not enter in the *POMIC* formula does not restrict our approach to be able to check for model parsimony.

About the precautions to use POMIC

Obviously, we should stretch the fact that as for comparing AIC values (Burnham and Anderson 2002) the *POMIC* values can only be compared among models tested against strictly identical set of field data. Additionally the same probability function estimates for the field data describing the patterns should be used, and the same way of calculating the probability function estimates of the simulation results should be applied. Another precaution, which was rarely considered in pattern-oriented modeling studies, is to have a

sampling design process within the model that reproduces the design used in the field. This last precaution is essential to *POMIC* since we made important assumptions out of this remark (particularly the one to use the sampling distribution function as a good indicator of the true distribution). However, this idea should also be applied when using other goodness of fit indicators such as mean-square deviation or regressions, because sampled field data not influenced by the sampling technique are almost inexistent. Actually, this consideration is also one of the main advances of our approach. Statistician or scientists used to information theories will see the *POMIC* as “only” a rough application of the K-L distance. The K-L distance in general could be applied to any situation of comparing two functions. We are here comparing a probability distribution function with another, the first being the sample that we try to reproduce, the second being the simulation results. But the advance is that we included the sampling process to obtain the simulation results, so that we are really comparing how well our model reproduces the sample distribution. This was to our knowledge never done in agent-based or individual-based modeling within or without a pattern-oriented modeling framework.

About the inverse-modeling with *POMIC*

Inverse-modeling is the exercise of estimating unknown model parameters from the goodness of fit results of simulations with different parameter values. One short-cut sometimes done in statistical modeling using information criteria is the model averaging of parameters over sets of models with different structure but including all the parameters in focus. We recommend strongly against this in the case of ABM/IBMs tuned with the *POMIC*. This, mainly because processes might not be always using a parameter in an identical way and therefore interact with other parameters influencing the pattern of focus in a same manner. Model parameters with identical names and biological purpose (e.g. in SIMOVIM the *MaxNeighD* is the maximum distance threshold of interaction with the closest neighbor in model version 2 to 4) might not have the same mathematical effect in different model version (e.g. *MaxNeighD* determine the use of random/ attraction or repulsion walk in the different SIMOVIM versions) and can therefore have different maximized likelihood estimates. The model averaging would be in this case completely misleading.

Conclusions

The *POMIC* is based on information theory and can therefore compute likelihood and weights of models given the data and the set of tested models. This allows to do strong inference on a set of models, but also (and eventually before) parameterization averaging for ABM/IBMs reproducing patterns at higher integration level. These aspects give to the pattern-oriented modeling approach an important improvement. While assessing a data set with a set of statistical model and AIC is looking for the most likely interconnection of parameters (sometimes representing processes), developing an ABM/IBM using the POM approach with *POMIC* could be compared to finding the actual “behavior” of individual parts that lead to a higher integration level emergent property. This new method, together with adaptation of new tools such as the Pareto evolve of Komuro et al. (2006) will definitely give agent and individual-based modeling developed in a POM context a new potential of inference on the understanding of “behaviors” of individual part of complex adaptive systems.

2.7 Acknowledgements

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2.9 Appendices

2.9.1 Appendix A

We describe here how to estimate the sampling probability functions $b(x|\theta^*)$ and the model results probability function $g(x|\theta)$. Let assume a rule-based stochastic model developed to reproduce the n observations of the variable x , with corresponding empirical measurements $X = x_1, x_2 \cdots x_n$. The simulation results of one replicate of the model with identical sampling process (with identical number of observations) are $Y = y_1, y_2 \cdots y_n$.

Estimating the sampling probability function of $n > 1$ field observations

We can draw a histogram of probability of observation of values of x from the measurements X with N_b categories defined by a vector of intervals $B = [X_{min}; B_2[, [B_2; B_3[\cdots [B_{N_b}; X_{max}]$ where each interval is of width ΔB . A function of probability of observation of x ($b(x)$) can be assumed as the continuous upper line of this histogram and could be considered as estimate of $b(x|\theta^*)$ (Fig. 2.2), so that:

$$\begin{aligned} b(x|\theta^*) &> 0 && \text{for any } x \in X \\ b(x|\theta^*) &= 0 && \text{for any } x \in]-\infty; X_{min}[\text{ or }]X_{max}; +\infty[\\ \text{and } \sum_{i=1}^n b(x_i|\theta^*) &= 1 \end{aligned}$$

Practically, the $b(x_i|\theta^*)$ of the observation x_i will be evaluated as the number of observations of X within the same category than x_i divided by n . Since we assumed in the "Background" part that the n observations of our sample were our entire universe to be reproduced by the model, we need the sum of these $b(x_i|\theta^*) = 1$ to assure that $b(x_i|\theta^*)$ would behave as a real probability function respecting the Kolmogorov axioms. For this reason this $b(x)$ function cannot be estimated as described in the following for the model result probability function.

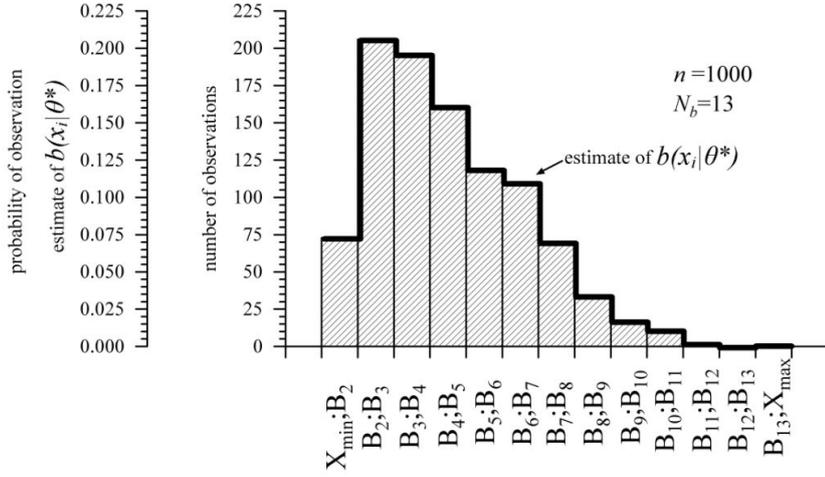


Figure 2.2: Fitting an estimator of the sampling probability density function to the histogram of observation of X .

Estimating the model results probability function

Using the same number N_b of categories and the same interval width ΔB than for the probability function of the field results, the simulation results Y can be also used to construct a histogram of probability of observations of y . As above, the upper line of this histogram could be considered as an estimate of $g(y)$. However, using such estimate as the probability function $g(x|\theta)$ would restrict a $POMIC$ value $< \infty$ only in a case of $[X_{min}; X_{max}] \in [Y_{min}; Y_{max}]$, which is uncomfortably harder to obtain as the n increase. To obtain a wider range where $g(x|\theta) > 0$ (leading to $POMIC$ values $< \infty$) a continuous function $g(y)$ could be fit to the probability histogram so that it is more likely returning > 0 for all x of X . For example, in the case that we know that the simulation results are known to be normally distributed, we can use a scaled probability density function of the normal distribution (pdf_{normal}) fitted to our simulation results. To get an estimator of the $pdf_{normal}(x)$ value of the field data given the model parameterization, we need only to calculate the mean of the simulation results (\bar{Y}), their standard deviation (SD_Y). We can then use this pdf_{normal} and scale it to probability of occurrence in the simulation results data set:

$$\begin{aligned}
 g(x|\theta) &= pdf_{normal} \times Scaling_P \\
 &= \frac{1}{SD_Y \sqrt{2\pi}} \exp\left(-\frac{(x - \bar{Y})^2}{2 \times SD_Y^2}\right) \times Scaling_P \quad (2.23)
 \end{aligned}$$

where $Scaling_P$ is a parameter calculated as:

$$Scaling_P = \max(g_h(x)) / \max(pdf_{normal}(x)) \quad (2.24)$$

where $g_h(x)$ is the function fit to the histogram described above, and $\max(\cdot)$ return the maximum value of both functions. This way of estimating the probability function is actually valid for any distributions of simulation results known to follow another specific distribution of which the probability density function can be calculated. In such case, the pdf of the specific distribution can be used instead of pdf_{normal} in equations 2.23 and 2.24.

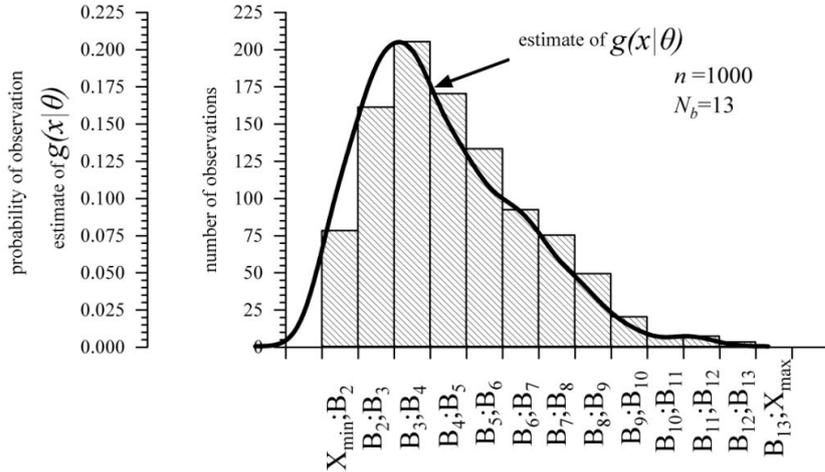


Figure 2.3: Fitting an estimator of the simulation results probability density function to the histogram of observation of Y with a density kernel estimator.

If we do not have a priori knowledge on the type of distributions of our simulations results, we recommend then to use a kernel density estimator of y values with a band width B_W so that $B_W = \Delta B/2$; and scale down these density estimates to the probabilities observed in the histogram of Y with the same technique as in equation 2.24. These transformed probability-density values will be the estimate of $g(x|\theta)$ for one replicate (Fig. 2.3). To estimate the likelihood to find a specific x_i value of the field data set given the model parameterization, we will estimate it as the $g(x_{closest}|\theta)$ value where $x_{closest}$ is the closest x value to x_i . For this reason, the density kernel estimator should have a B_W not too big to reduce the approximation error of this method.

2.9.2 Appendix B

Estimating the sampling probability function of $n = 1$ field observation

Assuming for e.g. that we want to reproduce a pattern of a spatial or temporal variable of which the values are considered independent. We would assume each observation as an independent variable of only 1 observation that should be reproduced by our IBM. Identically to the first case of appendix A (page 53), we need the sum of $b(x_i|\theta^*)$ to be equal to 1, and since $n = 1$, we could assume that $b(x_{\text{unique observation}}|\theta^*) = 1$.

Estimating the model results probability function reproducing $n = 1$ field observation

The simulation result should produce only one value of y per replicate $Y = y$. The likelihood to produce a precise x value given the model has then to be calculated out of the replicates results. Let assume the S replicates produce a vector T of unique observations per replicates $T = Y_1, Y_2 \dots Y_S$, the likelihood function of our model will then become the probability function fit to the vector T as described in Appendix A (page 53) for the simulation result probability function estimation depending if we know or not of an underlying distribution type for T .

2.9.3 Appendix C

We want to develop an unbiased estimator of goodness of fit of rule-based models including the processes θ leading to the distribution function g of x against a sample distribution function b of x influenced by the processes θ^* . We assume as loss function of doing this modeling exercise, the Kullback-Leibler (K-L) distance between both distributions:

$$\begin{aligned} I(b(x|\theta^*); g(x|\theta)) &= \int_{-\infty}^{+\infty} b(x|\theta^*) \log b(x|\theta^*) dx - \int_{-\infty}^{+\infty} b(x|\theta^*) \log g(x|\theta) dx \\ &= -H(b(x|\theta^*); b(x|\theta^*)) + H(b(x|\theta^*); g(x|\theta)) \quad (2.25) \\ &= E_b\{\log b(x|\theta^*)\} - E_b\{\log g(x|\theta)\} \end{aligned}$$

where the expectations (functions E) are taken with respect to the sample distribution function b , which is supposed here to represent the truth. Since the first term of the sum is constant for our modeling exercise, the K-L distance can be summarized as:

$$I(b(x|\theta^*); g(x|\theta)) = \text{constant} - E_b\{\log g(x|\theta)\} \quad (2.26)$$

since we have

$$-H(b(x|\theta^*); b(x|\theta^*)) = \text{constant}$$

In the AIC or other information criteria the expectation of log likelihood of the model $E \log g(x|\theta)$ to fit the data is taken with respect to the true distribution. In these cases, the data set is used to estimate the parameters with the maximum likelihood estimate (MLE) function related to the model to be fit, and also to estimate the goodness of fit of the respective model (Bozdogan 1987, Burnham and Anderson 2002). Consequently, the parameter distance of θ from θ^* can be estimated depending on the type of models, the number of parameters k in θ , the number of field observations n and the covariance among parameters. The approach consider then as risk function of doing modeling the expected K-L distance with respect to the true distribution, and this distance of θ from θ^* can indicate the bias factor bf of the general bias corrected information criterion (BCIC, Bozdogan 2000):

$$BCIC = -2 \log L(\hat{\theta}) + 2n \times bf \quad (2.27)$$

where $L(\hat{\theta})$ is the maximum likelihood of the model.

In our approach, the processes and parameters within them are not estimated with a maximum likelihood function considering the data to be fit to. So these biases bf can not be estimated and the whole approach of the AIC and other information criteria does not apply. But we want to fit the model to patterns that generally were already seen as of interest and therefore we do not intend to guess the true distribution function, but better to estimate the quality of our models in comparison to an expression of this true distribution given by the sample distribution. So coming back to the K-L distance as loss function, and its expectation with respect to the true distribution as the risk function, from equation 2.26 we have:

$$E_f\{I(b(x|\theta^*); g(x|\theta))\} = E_f\{\text{constant}\} - E_f\{E_b\{\log g(x|\theta)\}\} \quad (2.28)$$

The $E_f\{E_b\{\log g(x|\theta)\}\}$ expectation with respect to the true and sample distribution can then be assumed to be equal to $E_b\{\log g(x|\theta)\}$ only in respect to the sample distribution if we assume that: (1)the sample is a good representation of the truth and (2)redoing this modeling exercise should lead to the same models, i.e. the pattern-oriented modeling protocol (Wiegand et al. 2003) was well followed. Also, since $E_f\{\text{constant}\}$ is constant, we have to minimize an estimator of goodness of fit given by:

$$\begin{aligned} \text{Estimator} &= C - E_b\{\log g(x|\theta)\} \\ &= C - \sum_{i=1}^n b(x|\theta^*) \log g(x|\theta) \end{aligned} \quad (2.29)$$

This leads us to a preliminary proposition of *POMIC* that should be minimized:

$$POMIC = - \sum_{i=1}^n b(x_i|\theta^*) \log(g(x_i|\theta)) \quad (2.30)$$

And in general, to be able to transport the *POMIC* from one case of data fitting to another independently of the n , we divide *POMIC* by n :

$$POMIC = - \frac{1}{n} \sum_{i=1}^n b(x_i|\theta^*) \log(g(x_i|\theta)) \quad (2.31)$$

2.9.4 Appendix D

This appendix present the detailed results of the SIMOVIM inverse modeling phases.

Table 2.3: Results of the inverse modeling parameterization tests of the parameter of probability of individuals to change status from inactive to active (P_2) (in **bold**, the resulting best fitting P_2 value according to *POMIC*; in *italic* the expected best P_2 value of 0.25).

P_2	<i>POMIC</i> (Eq 2.20)	Δ_i (Eq 2.11)	w_i (Eq 2.14)
0.025	0.563	0.233	0.049
0.05	0.438	0.108	0.055
0.075	0.419	0.089	0.057
0.1	0.378	0.048	0.059
0.125	0.351	0.021	0.061
0.15	0.346	0.016	0.061
0.175	0.338	0.008	0.061
0.2	0.330	0.000	0.062
0.225	0.344	0.014	0.061
<i>0.25</i>	<i>0.355</i>	<i>0.025</i>	<i>0.060</i>
0.275	0.393	0.063	0.058
0.3	0.435	0.105	0.056
0.325	0.497	0.167	0.052
0.35	0.587	0.257	0.048
0.375	0.641	0.311	0.045
0.4	0.724	0.394	0.042
0.425	0.847	0.517	0.037
0.45	1.009	0.679	0.031
0.475	1.183	0.853	0.026
0.5	1.517	1.187	0.019

Table 2.4: Results of the inverse modeling parameterization tests of the parameter of maximum moved distance ($MaxMovD$) for the first version of SIMOVIM.

$MaxMovD$	$POMIC$ (Eq 2.21)	Δ_i (Eq 2.11)	w_i (Eq 2.14)
0.5	infinite	-	0.000
1	infinite	-	0.000
1.5	infinite	-	0.000
2	infinite	-	0.000
4	infinite	-	0.000
6	infinite	-	0.000
8	infinite	-	0.000
10	infinite	-	0.000
15	infinite	-	0.000
20	infinite	-	0.000

Table 2.5: Results of the inverse modeling parameterization tests of the parameter of maximum moved distance ($MaxMovD$) and threshold interaction with the closest neighbor ($MaxNeighD$) for the second version of SIMOVIM. Any parameter combination led to identical results.

$MaxMovD$	$MaxNeighD$	$POMIC$ (Eq 2.21)	Δ_i (Eq 2.11)	w_i (Eq 2.14)
0.5	2	infinite	-	0.000
1	5	infinite	-	0.000
1.5	8	infinite	-	0.000
2	10	infinite	-	0.000
4	12	infinite	-	0.000
6	15	infinite	-	0.000
8	18	infinite	-	0.000
10	20	infinite	-	0.000
15	22	infinite	-	0.000
20	25	infinite	-	0.000

Table 2.6: Results of the inverse modeling parameterization tests of the parameter of maximum moved distance (*MaxMovD*) and threshold interaction with the closest neighbor (*MaxNeighD*) for the third version of SIMOVIM.

<i>MaxMovD</i>	<i>MaxNeighD</i>	<i>POMIC</i> (Eq 2.21)	Δ_i (Eq 2.11)	w_i (Eq 2.14)
2	10	1.166	0.000	0.077
1.5	10	1.330	0.164	0.065
1	10	1.386	0.220	0.062
4	10	1.389	0.223	0.061
1	8	1.410	0.244	0.060
0.5	10	1.444	0.277	0.058
2	8	1.450	0.284	0.058
4	8	1.479	0.312	0.056
6	10	1.493	0.327	0.055
4	12	1.534	0.368	0.053
6	12	1.542	0.376	0.053
8	10	1.557	0.391	0.052
10	10	1.644	0.478	0.048
15	12	1.676	0.510	0.046
10	12	1.680	0.514	0.046
8	12	1.684	0.517	0.046
1.5	2	1.734	0.568	0.044
10	15	2.167	1.001	0.028
8	15	2.328	1.162	0.024
10	20	3.351	2.185	0.009
All other	combinations	infinite	-	0.000

Table 2.7: Results of the inverse modeling parameterization tests of the parameter of maximum moved distance (*MaxMovD*) and threshold interaction with the closest neighbor (*MaxNeighD*) for the fourth version of SIMOVIM.

<i>MaxMovD</i>	<i>MaxNeighD</i>	<i>POMIC</i> (Eq 2.21)	Δ_i (Eq 2.11)	w_i (Eq 2.14)
6	15	1.426	0.000	0.147
8	18	1.478	0.051	0.139
4	15	1.580	0.154	0.126
10	18	1.623	0.197	0.121
6	18	1.638	0.212	0.119
10	20	1.889	0.463	0.092
8	20	1.945	0.519	0.087
6	20	2.323	0.897	0.060
10	22	2.436	1.010	0.053
8	22	2.890	1.463	0.034
10	25	3.318	1.891	0.022
All other	combinations	infinite	-	0.000

Part I

Interspecific competition in Caribbean mangrove forests

Chapter 3

Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane



Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane

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3.1 Abstract

Mangroves are prone to receive frequently the full brunt of hurricanes and tropical storms. The extent of destruction and early regeneration are widely studied. The purpose of this study was to add a long-term view of mangrove regeneration and assess the potential effects on mangrove horizontal zonation patterns of catastrophic destruction. Hattie, a Category Five hurricane, hit the Belizean coast in 1961. It passed directly over the Turneffe Atoll where our study area, Calabash Cay, is located. At four sites of this island, mangrove forest structure was analyzed along transects parallel to the shoreline within zones delineated by species dominance and tree-height. We propose an index based on the Simpson index of diversity to express changes in the heterogeneity of the species dominance. Physical-chemical parameters and nutrient availability were also measured. The destruction levels were estimated by analysis of the distribution of diameter at breast heights of the bigger trees in the inland zones. Variations in species dominance among sites and zones could be explained by interactions of various factors. We also found that the different levels of destruction between the two sides of the island had a significant effect on current patterns of species and structural zonation at Calabash. We conclude that disturbance regime in general should be considered as a factor potentially influencing mangrove horizontal

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zonation patterns.

Key words: *Avicennia germinans*; Belize; hurricane disturbances; *Laguncularia racemosa*; long-term regeneration; mangrove forest dynamics; *Rhizophora mangle*; species dominance heterogeneity; Turneffe Atoll; zonation patterns.

3.2 Introduction

Mangrove forests line most of the world's tropical and subtropical coastlines. In this coastal position, mangroves receive the full brunt of hurricanes and tropical storms, which are a frequent form of disturbance in these latitudes. Tree mortality, tree species resistance, and early forest recovery immediately following hurricane destruction have been widely studied (e.g., Vermeer 1963, Stoddart 1963, Bardsley 1984, Roth 1992, Smith et al. 1994, Roth 1997, Imbert et al. 1998, Sherman & Fahey 2001, Baldwin et al. 2001, Imbert 2002). Rates of hurricane-related mortality in mangroves forests are significantly higher than for any other tropical forests (compared in Baldwin et al. 2001; see also Imbert et al. 1998). Some recent studies have also analyzed the impacts of these destructions on ecosystem functions such as peat formation (Cahoon et al. 2004) or woody debris accumulation (Krauss et al. 2005) within the decade following hurricanes. In contrast, few studies have examined the long-term recovery patterns (e.g., Smith & Duke 1987). In the studies carried out in the Caribbean, results of species resistance to hurricanes are contradictory. For instance, according to Roth, Smith, and Imbert (Roth 1992, Smith et al. 1994, Imbert et al. 1998, Imbert 2002) *Rhizophora mangle* is the least resistant to hurricane destruction. However, Sherman and Fahey (2001) found that *Avicennia germinans* is the least resistant. Regarding the relative importance of tree size, Roth (1992), Smith et al. (1994), and Baldwin et al. (2001) found a higher probability of destruction for intermediate and higher size classes. Other studies have shown either an inverse pattern (e.g., Imbert et al. 1998), or no difference in damage among size classes (e.g., Sherman & Fahey 2001).

The extent of forest damage depends on the intensity of the hurricane. Category One or Two hurricanes on the Saffir-Simpson Hurricane Scale (www.nhc.noaa.gov) should generally inflict less damage than Categories Three to Five. Nevertheless, the percentage of dead trees can also vary depending on site exposure. For example, Imbert (2002) and Sherman and Fahey (2001) found the highest levels of disturbance in zones close to the shoreline. (see also e.g., Roth 1992, Imbert et al. 1998). Baldwin et al.

(2001) reported also that the differences in levels of destruction at two sites in Florida depended on their relative position within the path of the eye of Hurricane Andrew. At Turneffe Atoll, Stoddart (1963) described that the mangrove forests on many small windward islands were completely destroyed by Hurricane Hattie, a Category Five storm that struck Belize in October 1961, while inside the atoll the vegetation damage were less important.

Delayed mortality is another source of variation in hurricane damage. Some mangrove trees are able to coppice (e.g., *A. germinans* and *Laguncularia racemosa*) and use their pre-hurricane reserves to create new tissues and foliage (Tomlinson 1986). However, if these trees are severely damaged, they do not live much more than 2 yr after the hurricane (see e.g. Sherman & Fahey 2001). The delayed mortality is not as high in mangroves as in other tropical forests (Imbert et al. 1998). Furthermore, mangrove forests appear less resistant but much more resilient than other tropical forests. Imbert et al. (1998) suggested that no Caribbean mangrove species are pioneers when compared to rainforests. However, mangrove species apparently present different adaptations for re-colonization strategies and wind resistance (Roth 1992), relating the effects of hurricanes to the mangrove dynamics and structure.

To our knowledge, no studies have yet documented the long-term effects of hurricanes on the horizontal zonation patterns of mangrove forests. Such patterns may refer to structural characteristics (structural zonation) or species dominance (species zonation). Structural zonation describes bands parallel to the shore differing in tree density, canopy height or tree diameters. Species zonation expresses zones successively encountered from offshore to inland with different monospecific composition or particular associations of few tree species. Several hypotheses have been expressed to explain the phenomena driving these patterns: plant succession (Davis 1940), geomorphological factors (Thom 1967), differential dispersal of propagules (Rabinovitz 1978), differential predation on propagules (Smith 1987), interspecific competition (Ball 1980) and species-specific physiological adaptations to gradients (Macnae 1968, for review see Smith 1992). In Belize, differential predation on propagules is not responsible for differences in species zonation (McKee 1995a). McKee (1993) found that physiological adaptations best explain zonation patterns in Belizean mangroves. Together with the species-specific physiological adaptations to gradients of salinity and tidal influence, nutrient availability plays an important role in Caribbean mangrove zonation (Feller et al. 2003).

The main objective of this study was to determine whether perturbations such as hurricanes interact with other possible explanatory phenomena mentioned above to have an effect on these horizontal zonation patterns in

mangrove ecosystems. The second aim was to document the long-term effects of large-scale destruction on forest structure and to propose some recovery pathway scenarios. The offshore Belizean mangrove islands in Turneffe Atoll provided an ideal location for these investigations since they were previously destroyed by Hurricane Hattie more than 40 yr ago, and the occurrence of only four tree species provides a particular but relatively simple forest system.

3.3 Methods

3.3.1 Study area and sites

This study was conducted at Calabash Cay (also sometimes referred as the “Main Calabash Cay” of a “Calabash Cays” group), on the eastern side of Turneffe Atoll, one of the three Belizean atolls (Fig. 3.1). It is located approximately 34 km east of the MesoAmerican Barrier Reef and about 50 km from the mainland. Calabash Cay is almost 2 km long and about 1 km at its widest point. It includes an inner lagoon that is linked to the Turneffe lagoon waters by a small creek on the north end of the island (Fig. 3.1). It is fringed by mangroves on all its inner and outer coasts with the exception of part of the eastern side. The tidal range is microtidal (average range < 30 cm) and is classified as mixed semidiurnal.

The climate is tropical to subtropical, with clearly distinct rainy and dry seasons. The annual rainfall range is below the 2020 mm per year of Belize City but above 1500 mm (C. Piou, pers. obs.). Average maximum air temperatures vary from 32°C in summer (March to September) to 28°C in winter (October to February). Average minimum temperatures vary with the same monthly pattern from 24°C to 20°C. The climate is influenced by cold fronts (or “Northerns”) coming from North America during the winter months. Between July and November, hurricanes in the Caribbean Region increase the occurrence of heavy rain and strong to catastrophic winds.

On 31 October 1961, Hurricane Hattie, a Category Five hurricane, hit the Belizean coast. The eye of this hurricane went from east north-east to west south-west over Turneffe Atoll with winds over 260 km/hr. The intensity, wind direction, wave action, and the storm surge destroyed all of the human habitations and most of the mangrove forests of Calabash Cay. According to Stoddart (1963) who visited Turneffe in 1962, Big Calabash, a small island ~ 300 m to windward of Calabash Cay, was completely cleared of any mangroves by Hattie. Based on Stoddart’s description, a gradient in severity of destruction from east to west was expected for mangrove forest

at Calabash Cay. Specifically, Stoddart (1963) described that defoliation of mangrove stands was less severe and regeneration was already occurring in the interior part of Turneffe Atoll by early 1962. Calabash Cay has a large inner lagoon, which is considered a natural shelter by the local population. The wave action and the tidal hurricane surge were weaker inside the inner lagoon than outside. Since the human settlements were destroyed and not rebuilt after Hattie, the regeneration of the mangrove forests of Calabash Cay was not influenced by any anthropogenic activities since 1962. Although tropical storms and lightning strikes could have induced the death of individual trees, no other hurricanes or catastrophic perturbations have affected substantially the Calabash mangroves since Hattie. The gradient of disturbance hypothesized by Stoddart (1963) in a relatively short distance around Calabash makes this area ideal for the main objective of this study.

Four study sites were selected around Calabash along the proposed disturbance gradient. These sites were labeled A to D (Fig. 3.1). All sites extended from the fringing mangrove forest along the water's edge to the high intertidal margin where buttonwood (*Conocarpus erectus*) thickets dominated adjacent to the upland terrestrial forest. Preliminary surveys were conducted to determine zones within these sites depending on both the apparent structural and species zonation patterns. Site A was located on the northeast side of Calabash where four zones were defined from the shoreline inland. Site B was located on the northernmost point of Calabash and four zones were defined. Site C was situated on the northwest side of Calabash and extended from Orchid Creek to the upland area with six different zones. Site D was located on the east side of the inner lagoon and had three mixed zones.

3.3.2 Forest measurements

Mean diameter at breast height (DBH), tree height, density, and species frequencies were measured by the point centered quarter method (PCQM) transects laid within each zone of each site between November 2002 and February 2003. In order not to measure the same tree twice, the distance between points of the PCQM transects varied between 2 m in the dwarf areas to 12 m in tall basin forests. Each of the PCQM transects consisted of 21 points for a representative measurement of the studied area (Cintrón & Schaeffer-Novelli 1984).

3.3.3 Physical-chemical survey

Porewater salinity and pH were measured with a YSI ©556 Multi-Probe-System at three different periods: 24-30 November 2002, 6-9 February 2003,

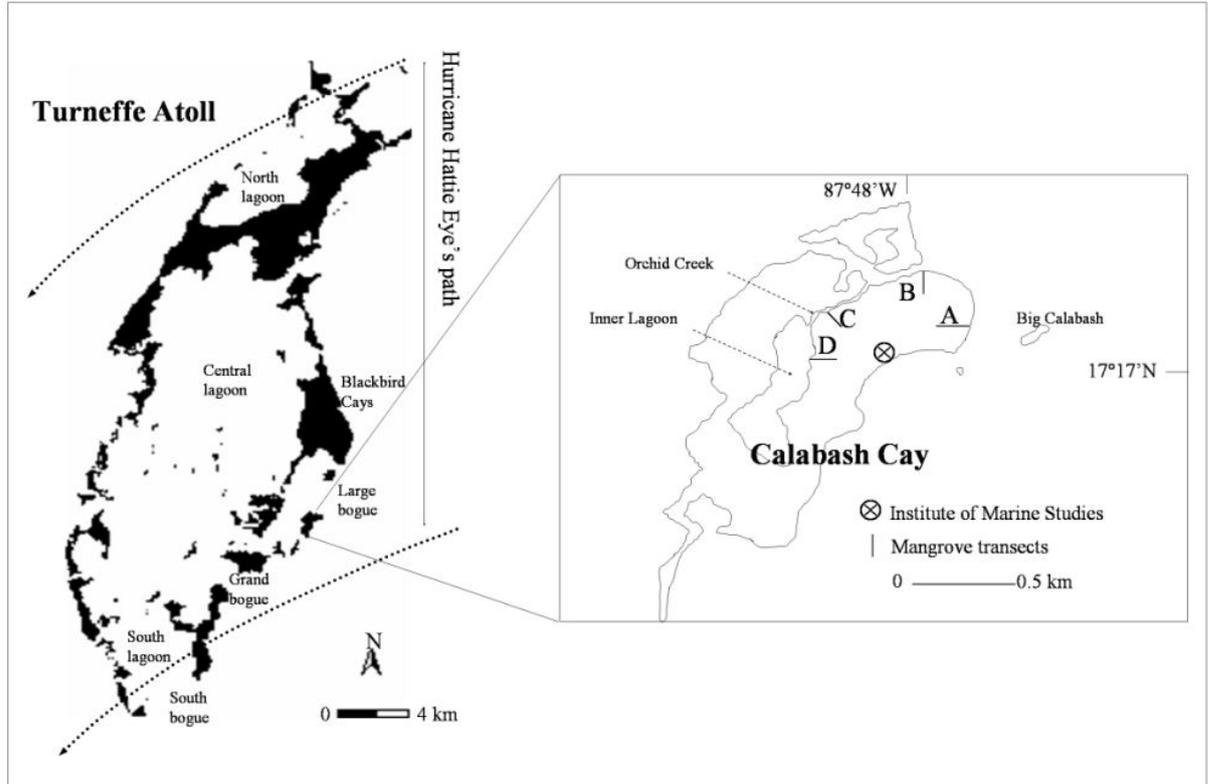


Figure 3.1: Turneffe Atoll with Hurricane Hattie eyes path and Calabash Cay with localization of the sites (modified from Garcia & Holtermann 1998).

and 27 February 2003. Tidal measurements were made 13-22 February 2003. Tide tables and several overnight measurements in a row were used to estimate a February maximum tidal level for each station. A yearly maximum tidal level was computed by extrapolation of these February maximum tidal levels in conjunction with the yearly tide tables. The slope of the elevation change within each zone was also calculated with the following formula:

$$slope = \frac{H_3 - H_1}{Dist_{1-3}} \times 100 \quad (3.1)$$

where H_1 and H_3 were the relative elevation of the first and last point of each zone, respectively, and $Dist_{1-3}$ was the distance between these two points.

As a measure of site fertility, the nutrient resorption efficiency and leaf biomass production per unit of nutrient were calculated as an indirect way to determine trends of nutrient availability, as described in Feller et al. (1999). Leaves were collected 20-22 February 2003. In each zone where present,

four samples of three to five pairs of leaves of *R. mangle* were harvested. A pair was composed of a mature leaf and a ready-to-fall senescent leaf from the same twig. Digital images and image analysis software (SigmaScan Pro 4.0) were used to measure leaf area. All samples were oven-dried at 70°C, weighed, and ground to pass through a 0.38mm mesh screen. We measured nitrogen (N) and phosphorus (P) concentrations in the green and senescent leaves and calculated nutrient resorption efficiency and biomass production per unit of nutrient invested for each experimental tree. Resorption efficiency (*RE*) was calculated as the percentage of N and P recovered from senescing leaves before leaf fall (Chapin III & Van Cleve 1989):

$$RE = \frac{N \text{ or } P \text{ (mg.cm}^{-2}\text{)}_{\text{green leaves}} - N \text{ or } P \text{ (mg.cm}^{-2}\text{)}_{\text{senescent leaves}}}{N \text{ or } P \text{ (mg.cm}^{-2}\text{)}_{\text{green leaves}}} \times 100 \quad (3.2)$$

Biomass production per unit of nutrient was calculated as the inverse of the nutrient concentration in senescent leaves (nutrient use efficiency, *NUE* in g biomass/g N or P).

3.3.4 Indicators of destruction level

No direct information was available to estimate differences of mangrove destruction among sites during Hurricane Hattie. Therefore, an indirect measurement was necessary to extrapolate from the standing trees considered older than 41 yr to compare an estimated destruction level among the four sites. From these estimates, a qualitative variable of “complete” or “incomplete destruction” was attributed to each site.

In the most inland mangrove zone, named here hinterland zone, of the four sites, belt-transects of 60 m long and 10 m width were established. The hinterland zones were chosen to make certain that the trees measured were in a comparable physical-chemical situation. Within these belt-transects, all trees with DBH more than 20 cm were measured. The distribution patterns of these large trees were used to detect extraordinary old or large trees seen as outliers in the right side of the distribution. These outliers were then used as proxies of destruction levels of the four different sites, assuming that they represent the trees older than 41yr.

In the fringe (i.e., the first zone along the water’s edge) and dwarf zones of site C, a tree aging technique was adapted from Duke and Pinzón (1992) based on leaf scar production to estimate the possible destruction level of this forest. An estimation of leaf scars produced by dwarf *R. mangle* of Turneffe Atoll was 4.1 scars per year (I.C. Feller, unpublished data). This number

was rounded to 5 to keep an error range and a robust estimate of tree age. Leaf scars were counted from the topmost apical leaves to the bottom of the trees for all stems present in three $1 \times 1\text{m}$ plots. Stems from an individual tree having more than 205 scars were considered to be older than 41 yr. The percentage of trees > 41 yr was calculated from these measurements.

3.3.5 Data analysis

The PCQM results were used to calculate an importance value (IV) for each of the four species per zone as described in Cintrón and Novelli (1984). IV was based on relative density, relative dominance and relative frequency of each species. Consequently, the sum of the IV of all four species was equal to 300 for each zone. To summarize the IV variation between zones and sites and to consider all species at the same time, we developed an index of species dominance heterogeneity (I_{SDH}) based on the following equation, adapted from the reciprocal index of Simpson (Hill 1973):

$$I_{SDH} = \frac{300 \times (300 - 1)}{\sum_{i=1}^q (IV_i \times (IV_i - 1))} \quad (3.3)$$

where IV_i is the importance value of the species i and q the number of species. I_{SDH} is comparable to a species diversity index of second order of entropy because it would increase with a higher number of species but give more weight to the evenness in IV . The index was used because it incorporates the relative importance of species in term of forest structure instead of the number of individuals. Thus dominance change would not only be a question of numbers of individuals, but also of space occupied by each species.

Non-parametric Spearman R correlation analyses were conducted to investigate the relationships between the physical-chemical factors including the nutrient availability indicators and the different forest structure variables (excluding I_{SDH}). A factor analysis with principal component extraction and varimax rotation was carried out to group linear correlations among the four nutrient variables. Scores of the two principal factors were used as explanatory variables for the further analyses. To investigate the factors influencing the variation of the I_{SDH} , a general linear model analysis using Type V decomposition was used, followed by a general regression model analysis with backward stepwise selection of variables. The following continuous independent variables were considered for both analyses: mean recorded salinity, maximum tidal level, mean pH, slope, and the two synthetic factors of nutrient use and resorption efficiencies. The qualitative variable of destruction was also used as categorical factor in these analyses. The I_{SDH} and slope

values were square root($\arcsin(x/4) + \text{constant}$) transformed to get closer to normality.

3.4 Results

3.4.1 Forest measurements

The canopy height and DBH at all sites showed general increases from the fringe zone to the hinterland (Fig. 3.2). However, the resulting structural zonation patterns among sites were different. For example, trees at site C were dwarf over a 60 m wide area followed by a 15 m tall forest whereas trees at site A were relatively homogeneous across the forest. Another main difference among the sites was seen in the species zonation pattern (Fig. 3.2). As a general pattern, *R. mangle* dominated the fringe zone of all sites. The basin zones were occupied mainly by *A. germinans* in sites B, C and D. These sites were dominated by *L. racemosa* in the hinterland zones. In contrast, *R. mangle* was dominant in all zones at site A.

Species dominance heterogeneity (I_{SDH}) varied significantly among zones and sites (Fig. 3.2). Sites C and D were more heterogeneous than sites A and B. The pure dominance of *R. mangle* in the zones 1 and 2 of site A was not found in other parts of the island except in the fringe and the first dwarf zone of site C. Also, the only pure area of *A. germinans* was found on site B. An herbaceous species, *Batis maritima*, was found on both sides of the island and in different zone types.

3.4.2 Physical-chemical measurements

The salinity was relatively homogeneous at site A (Table 3.1). The maximum salinities were measured in *A. germinans* basins at site B, C and D. The minimum values were recorded in hinterland zones of all sites. The pH values of site A and B were neutral at the fringe and hinterland, and slightly lower in the central zones probably linked to anoxic conditions (Table 3.1). For sites C and D, pH values were generally increasing toward the hinterland zones. In sites A and B, the first and last zones had higher slope values compared to the central zones, which were almost completely flat. Site D had in general the same pattern whereas the topography was more varying at site C (Table 3.1).

Nitrogen use efficiency ($NUE - N$) varied slightly, leading to few significant differences among zones and sites (Fig. 3.3). The highest values occurred in site C, particularly in the dwarf zones. Phosphorus use efficiency

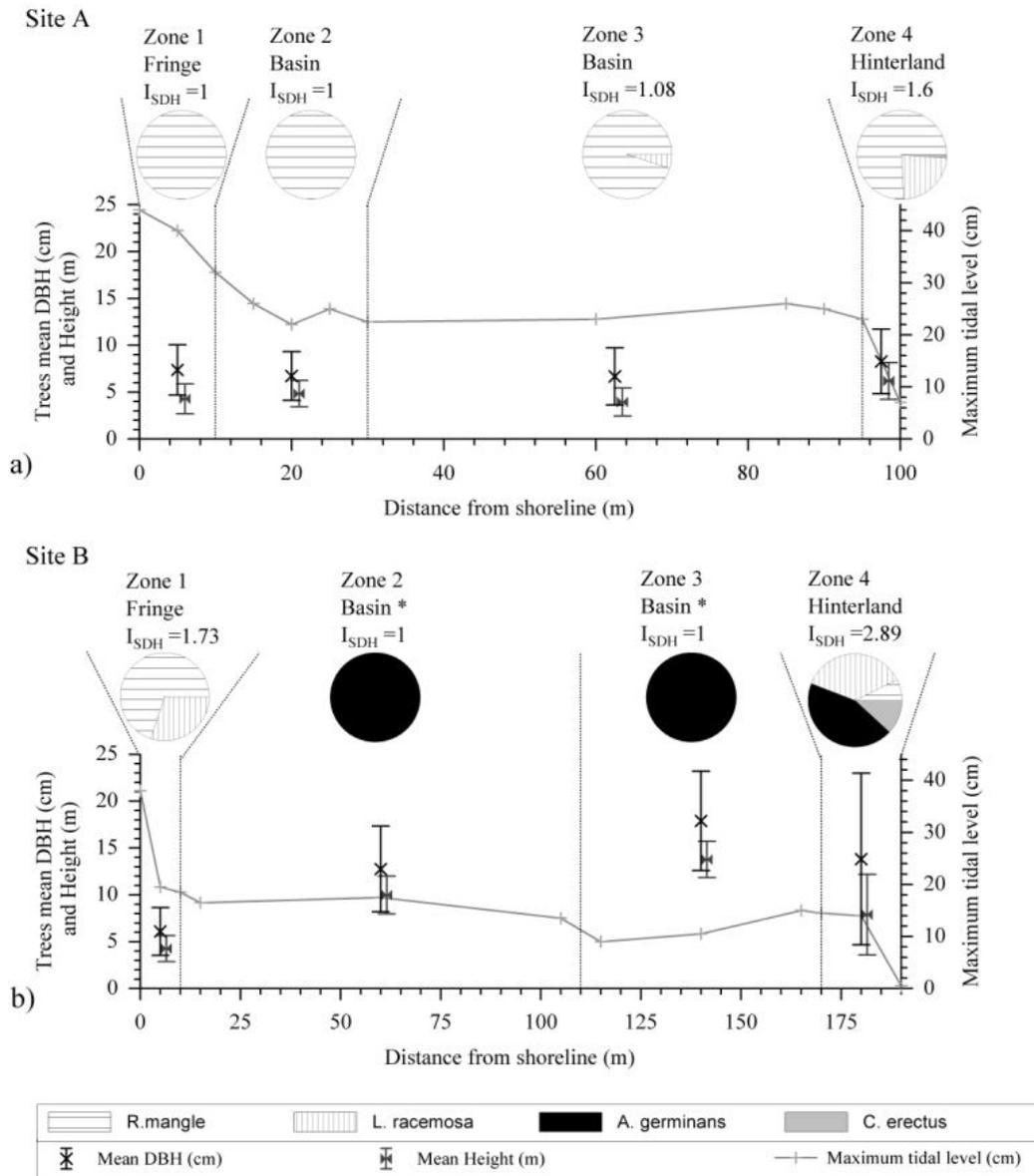


Figure 3.2: Mangrove forest structure of the different sites (A – D respectively). Zones are named according to position and type of structure (*indicate presence of *Batis maritima* on the ground). I_{SDH} values indicate the corresponding Index of species dominance heterogeneity. Pie charts show the species composition. Line graphs show trees mean DBH, mean canopy height per zone (error bars represent standard deviations), and profile of maximum height of tidal level at equinoxes spring high tide (in cm above ground).

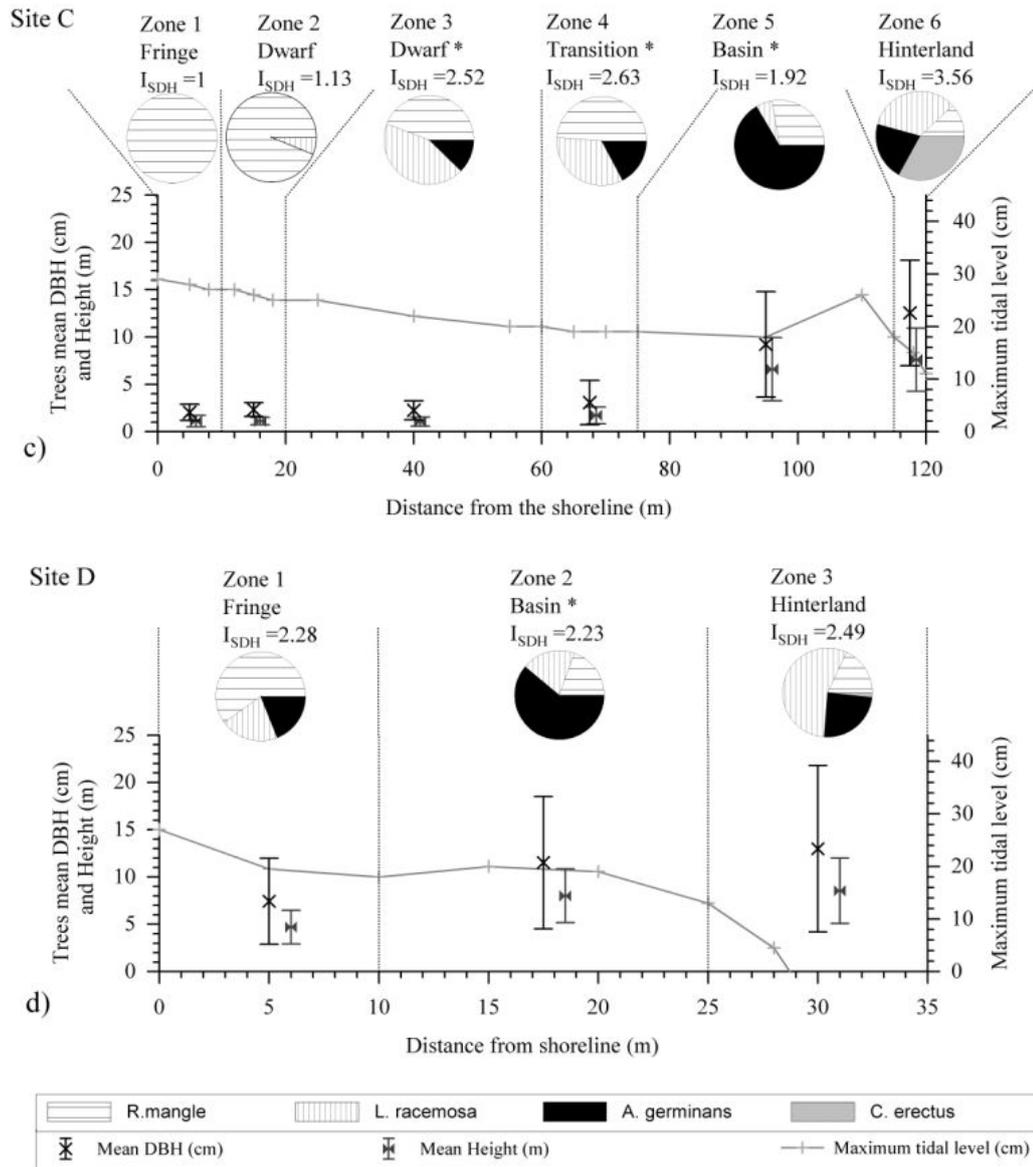


Figure 3.2 continued.

Table 3.1: Physicochemical measurements results per sites and zones. (Values are mean salinity \pm SD, expressed in practical salinity units (psu); mean pH \pm SD; S = slope of zone ground, in %.)

Zones		1	2	3	4	5	6
Site A	psu	37.9 \pm 0.4	36.9 \pm 1.5	37.7 \pm 2.0	37.0 \pm 3.3		
	pH	6.6 \pm 0.2	6.4 \pm 0.05	6.4 \pm 0.1	7.0 \pm 0.4		
	S	1.2	0.1	-0.06	1.8		
Site B	psu	38.9 \pm 0.9	45.1 \pm 8	46.0 \pm 10.6	39.6 \pm 10.9		
	pH	6.7 \pm 0.6	6.8 \pm 0.3	6.5 \pm 0.1	6.9 \pm 0.2		
	S	1.95	0.03	-0.12	0.7		
Site C	psu	40.5 \pm 2.7	44.9 \pm 2.8	46.1 \pm 5.0	39.7 \pm 5.1	42.0 \pm 9.0	22.8 \pm 9.1
	pH	6.6 \pm 0.1	6.6 \pm 0.3	6.7 \pm 0.2	6.5 \pm 0.1	6.8 \pm 0.3	7.1 \pm 0.1
	S	0.25	0.33	0.17	0.1	-0.2	1.4
Site D	psu	40.6 \pm 6.3	44.7 \pm 6.5	21.6 \pm 5.1			
	pH	6.5 \pm 0.2	6.9 \pm 0.1	7.3 \pm 0.2			
	S	0.9	0.7	2.07			

($NUE - P$) was also very high in these dwarf zones of site C. For all sites, $NUE - N$ and $NUE - P$ were generally higher in zone 1 and decreased going landward. There were no significant differences in N resorption efficiency ($RE - N$) among the sites (Fig. 3.4). Similar to patterns of $NUE - N$ and $NUE - P$, P resorption efficiency ($RE - P$) was highest in the dwarf zones and with lowest values in the inland zones at sites B, C and D (Fig. 3.4). The variations in NUE and RE among the sites and zones were synthesized with factor analysis (Table 3.2), which confirms tight correlation of both $NUE - N$ and $-P$ and $RE - P$.

Table 3.2: Factor loadings of nutrient use variables factor analysis with principal component extraction method and varimax rotation (marked loadings are > 0.70).

	Factor 1	Factor 2
$NUE - N$	0.738	0.490
$NUE - P$	0.958	-0.098
$RE - N$	0.023	0.978
$RE - P$	0.901	0.153
Eigenvalues	2.273	1.230
Prop. of Total Var.	0.568	0.307

3.4.3 Indicators of destruction level

In the belt transects of the hinterland zones of sites A and B, the frequency distribution of DBH of trees > 20 cm decreased continuously going toward

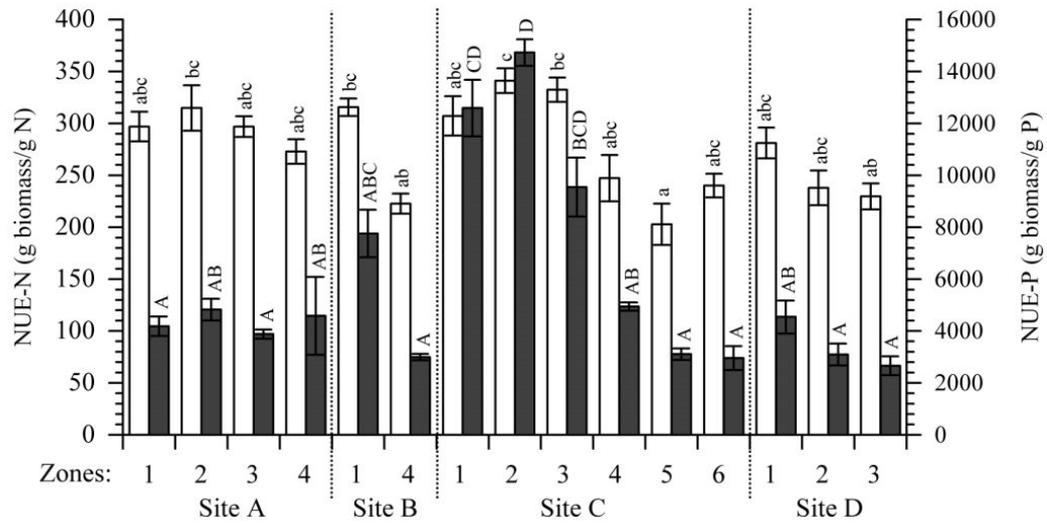


Figure 3.3: *Rhizophora mangle* leaves nutrient use efficiency of nitrogen (white bars) and phosphorus (filled bars) in grams of created leaf biomass/g of N or P (error bars = SE). The x-axis represents the different sites and zone numbers. Letters show the homogeneous groups (*Posthoc* analysis Sheffé test).

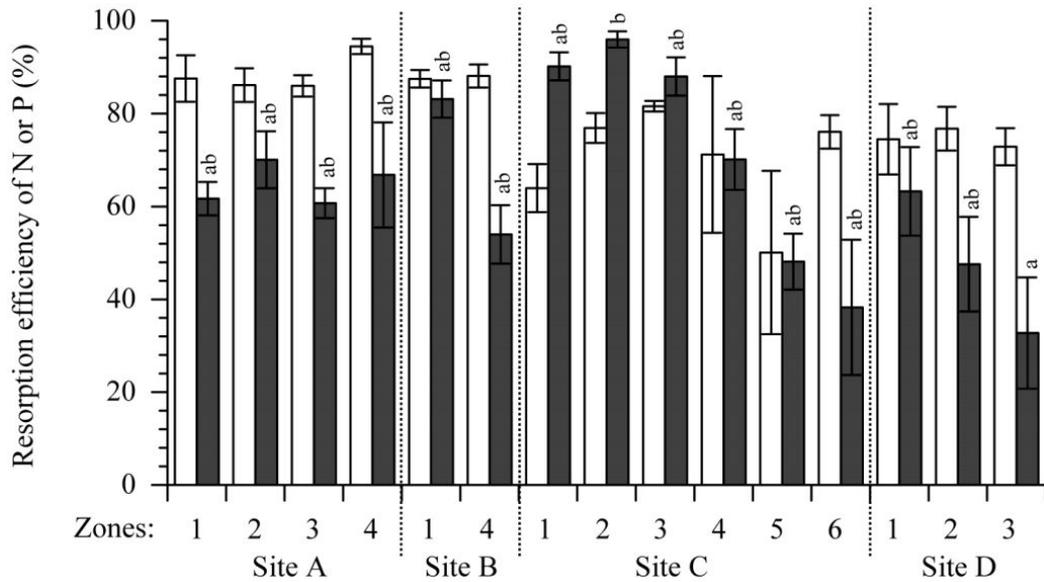


Figure 3.4: *Rhizophora mangle* leaves resorption efficiency of nitrogen (white bars) and phosphorus (filled bars) in percentage (error bars = SE). The x-axis represents the different sites and zone numbers. Letters show the homogeneous groups (*Posthoc* analysis Sheffé test).

bigger size classes (Fig. 3.5). However in the hinterland zones of sites C and D, the distribution included a few outliers with DBH > 55 cm. The largest trees in sites A and B had DBH < 37 cm, which together with the continuous decrease, provided evidence that the trees in those sites had grown subsequent to Hurricane Hattie. On the contrary, the frequency distribution of DBH of sites C and D was discontinuous between 45 cm and 55 cm. The few large trees at the end of the distribution survived Hattie and were thus > 41 yr old. Additionally, in zones 1 and 2 at site C, more than 61 percent of dwarf trees were > 41 yr.

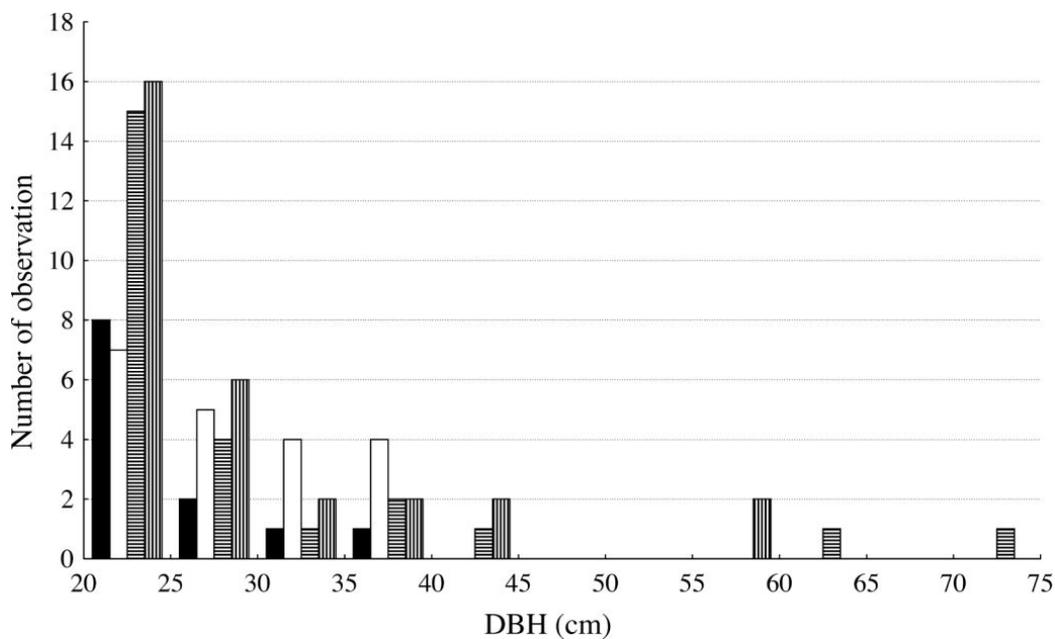


Figure 3.5: Trees DBH class distribution (only DBH > 20 cm) in the last zone of each sites (Site A: black filled; Site B: white; Site C: horizontal stripes; and Site D: vertical stripes).

All these observations suggest that Hattie caused complete destruction of the mangrove forest at sites A and B, whereas remnants of the original forests still existed across the forests at sites C and D, indicating incomplete destruction. This information was used to generate a dummy variable of two destruction levels: for sites A and B, 0=complete destruction during Hattie, for sites C and D, 1=incomplete destruction during Hattie.

3.4.4 Statistical analyses

The Spearman correlation analyses showed that the importance values (*IV*) of *R. mangle* were negatively correlated to the pH and positively to $NUE - N$, $NUE - P$ and $RE - P$. *IVs* of *A. germinans* were negatively correlated to $NUE - N$, $NUE - P$ and $RE - P$ but positively to the maximum recorded salinity. *IVs* of *L. racemosa* were negatively correlated to the maximum tidal level and positively to the slope and pH. *IVs* of *C. erectus* were negatively correlated to the maximum tidal level, the mean salinity, $NUE - N$, $NUE - P$ and $RE - P$ but positively to the slope and pH (Spearman correlation test, $P < 0.05$ in all cases). Additionally $NUE - N$, $NUE - P$ and $RE - P$ were negatively correlated with DBH and tree height and positively correlated with tree density (Spearman correlation test, $p < 0.01$ in all cases).

The general linear model constructed with all the variables did not explain significantly variations of the index of species dominance heterogeneity (I_{SDH}) (test whole GLM model vs. residual, Multiple R=0.812, F=2.483, $p=0.102$). However, within this model, the destruction indicator dummy variable had a significant effect on the I_{SDH} (GLM univariate significance; F=5.158, $p=0.049$). None of the other variables (i.e., salinity, tidal level, pH, slope, and nutrient availability factors) had a significant influence on the I_{SDH} . On the contrary, the general regression model constructed with a backward stepwise selection and selecting the destruction indicator dummy variable and the first factor of nutrient availability indicator (Table 3.3), explained a significant proportion of the variance of I_{SDH} (test whole GRM model vs. residual, Multiple R=0.718, F=7.450, $p=0.006$).

Table 3.3: Univariate tests of significance and summary of parameters of the general regression model with backward stepwise selection of explanatory variables on the I_{SDH} variations (marked factors are significant at $p < 0.05$).

	SS	df	MS	F	p	Parameter	Std Error
Intercept	0.735	1	0.735	1.515	0.239	-0.208	0.169
Maximum Tidal Level	Pooled	0					
Mean Salinity	Pooled	0					
Mean pH	Pooled	0					
Slope	Pooled	0					
Factor 1 Nutrients	3.934	1	3.934	8.113	0.013	-0.559	0.196
Factor 2 Nutrients	Pooled	0					
Destruction	4.203	1	4.203	8.667	0.011	-0.502	0.170
Error	6.789	14	0.485				

3.5 Discussion

Forest measurements results showed clearly different horizontal zonation patterns at Calabash Cay. Firstly, the structural zonation pattern indicated by DBH, tree height, and forest density differed at each site. Correlation analyses suggested that these patterns were related to N use efficiency, P use efficiency, and P resorption efficiency. According to the findings of Feller (1995) and Feller et al. (2002, 2003), these values were indicative of nutrient availability. The species zonation patterns were also clearly different from sites to sites. *Rhizophora mangle* was more dominant in low nutrient availability and acidic areas. Similarly, *Avicennia germinans* dominated more in high salinity and high nutrient availability areas, and *Laguncularia racemosa* in higher intertidal, steeper and more neutral to basic zones. The restriction of *C. erectus* only in the hinterland zones demonstrated the adaptation of this species to rarely inundated areas (Tomlinson 1986). These trends fit well with other studies in the Caribbean. They suggested that differences in propagules dispersal (Rabinovitz 1978, Jiménez & Sauter 1991), geomorphological factors (Thom 1967), as well as physiological adaptations to gradients across the intertidal zone (Macnae 1968, or e.g., McKee 1995a, McKee 1995b) were interacting factors driving zonation patterns in Calabash Cay.

According to Stoddart (1963), the vegetation of inner parts of Turneffe was less damaged by Hurricane Hattie than the vegetation of outer sites. Both proxies used to indicate destruction levels in this study supported this observation 41 years later: the distributions of all trees with dbh > 20 cm showed that no old trees (right side outliers) existed in the seaward sites A and B, but some big hollow, remnant trees older than 41yr were found in the inner sites C and D. Secondly, the number of scars indicating the age of dwarf trees also showed incomplete destruction in a sheltered position on the west side of Calabash. The percent of dwarf trees older than 41yr suggested that the dwarf mangroves of Calabash Cay were the trees that best resisted Hurricane Hattie. These findings were consistent with other observations from the Caribbean (Smith et al. 1994, Lugo 1997) and Australia (Bardsley 1984). During Hattie, the high water level due to the storm surge would have covered these small individuals, preventing them from being blown down by strong winds. If these trees had been exposed to wave action, it is likely that they would have been killed as the fringing zones of most hurricane-destroyed sites (e.g. Imbert 2002). Thus, the survivability of the dwarf trees makes them potential sources of propagules for re-colonization processes after large perturbations.

The index of species dominance heterogeneity (I_{SDH}) showed differences among zones and sites. One of the general trends for each site was that the

hinterland zone had the maximum I_{SDH} value. This trend resulted from the higher possibility of finding pure *R. mangle* or *A. germinans* stands in the lower intertidal zones than in the hinterland where *L. racemosa* was frequently mixed with *C. erectus*. Beside these intra-site variations, the I_{SDH} at the east side of the island (i.e., the exposed part that sustained the most damage from Hattie) was more homogeneous than the west side (sheltered part). Our statistical results with the GLM model showed the importance of the destruction indicator to these forest heterogeneity differences. The GRM model also included the factors indicating nutrient availability, which could be related to two aspects of forest heterogeneity. First, P use efficiency and resorption efficiency increased from the fringe to the upper zones, as did the I_{SDH} . Second, N use efficiency was highest at sites where *R. mangle* dominated, leading to a low I_{SDH} . These relationships supported the hypothesis that nutrient availability was important to species dominance. Yet, only the model including both the nutrient availability and the destruction indicator explained the differences of forest heterogeneity between the two sides of Calabash. These results suggested that forest dynamics at Calabash were influenced by the remnant forest that survived Hattie. A possible scenario was that the surviving *A. germinans* and *L. racemosa* as well as the dwarf *R. mangle* trees on the western side of the island served as a reservoir for propagules on the nearby areas. In combination with external propagules, this could have resulted in a relatively rapid re-colonization of Calabash. Succession modified by the presence of the larger trees might have increased the spatial patchiness by competition effects. We observed that some *R. mangle* trees developed as an understory in *A. germinans* basins at the sheltered sites, which indicated that this complex phenomenon was not finished yet. *Rhizophora mangle* may eventually out-compete the two other species in some zones. In contrast, on the eastern sites, succession and out-competition probably happened according to the species characteristics to abiotic conditions. This would have led to more homogeneous zones with clearer partitioning of the species along the intertidal. The example of Calabash Cay having the most heterogeneous sites on the least destroyed sites except for the dwarf areas was contradictory to what Baldwin et al. (2001) predicted for Biscayne Bay (Florida). However, their observations of the regeneration of mangrove sites were only 7yr after Hurricane Andrew, and illustrated the influence of several herbaceous species on the early regeneration pathways. The herbaceous species present in Calabash Cay were found in both heterogeneous and homogeneous forest. Our study was consistent to Imbert (2002) who found that the number of surviving trees influenced the recovery pathways and succession. All these studies showed that remnant vegetation plays an important role for the recovery of mangrove forest after

hurricane destruction.

To conclude, this study suggests that disturbance intensity can influence the recovery pathways and succession in mangrove forests. Detailed quantitative data on forest structure before and after disturbance and following regeneration processes would provide stronger evidence of this relationship. However, the example of Calabash Cay mangroves showed that the perturbation regime should be considered when interpreting horizontal zonation patterns of mangrove forests.

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Chapter 4

Modeling the effect of hurricane disturbances on mangrove forest diversity



Modeling the effect of hurricane disturbances on mangrove forest diversity

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4.1 Abstract

Questions: What are the factors influencing tree species diversity of mangroves, an example of species-poor systems? What are the respective importance and interactions of these factors? Is the intermediate disturbance hypothesis applicable to mangroves?

Methods: We used the spatially explicit individual based model KiWi to investigate the effects on species diversity of perturbation frequency and intensity, different abiotic conditions, and interspecific competition simulated at individual level. The simulated system considered the three Caribbean mangrove species: *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*, applying species-specific growth and mortality characteristics. Firstly, effects on species dominance of different abiotic conditions represented as nutrient availability and pore-water salinity were tested with two competition scenarios. Secondly, the effect of perturbation frequency and intensity were investigated with selected abiotic conditions.

Results: Abiotic conditions influenced species dominance and in extreme cases excluded some species. Abiotic and competition settings controlled the succession dynamics and the response of species dominance to perturbation regimes. A response consistent with the intermediate disturbance hypothesis was observed only with a configuration of plant interaction in which one species behaved as a pioneer so that succession occurred by competitive

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exclusion.

Conclusions: We suggest that the successional dynamic interacting with the intensity and timing of perturbations will determine whether mangrove tree diversity will follow an intermediate disturbance hypothesis pattern or not. For mangroves, this successional dynamic is site-specific depending on abiotic conditions and species configurations.

Key words: individual-based modeling, KiWi model, intermediate disturbance hypothesis, species dominance, perturbation regime, species-poor systems

Abbreviations: FON= Field of Neighborhood; I_{SDH} = index of species dominance heterogeneity; RNA = Relative nutrient availability; psu= practical salinity units; IDH = Intermediate disturbance hypothesis; dbh= diameter at breast height

4.2 Introduction

For several decades, plant ecologists have tried to understand the processes implicated in species diversity variation (e.g. Chust et al. 2006 see reviews by Loreau et al. 2001, Barot & Gignoux 2004, Vellend & Geber 2005). Among these processes, perturbations have been considered of high importance and led to an on-going debate on the intermediate disturbance hypothesis, which states that species richness is maximized at intermediate levels of disturbances (Connell 1978; see reviews by Mackey & Currie 2001, Sheil & Burslem 2003, Shea et al. 2004). The situation of mangroves along tropical coastlines favors potential damage by major destruction events such as hurricanes or tropical storms (Imbert et al. 1998). Smith and Duke (1987) addressed the question of disturbance effects on mangrove tree diversity in Northern Australia. They showed that tree species richness decreased with increasing hurricane frequency. However, very few studies have analyzed changes in mangrove species composition in relation to perturbation regime (Baldwin et al. 2001, Piou et al. 2006), and none evaluated the implicated processes behind these effects. A straightforward explanation for this lack of consideration is the low number of tree species on mangrove systems. For example, in the Caribbean region, which is a hot spot of hurricane impacts, only three to four true mangrove species are found. Thus, studies on tree species diversity are mostly seen as superfluous in this system.

However, considering species diversity as an expression of species richness and evenness (Kempton 1979), systems with only three species could

vary also in species diversity. Piou et al. (2006) used an adaptation of the Simpson's Reciprocal index of species diversity (Simpson 1949, Hill 1973) to determine that the destruction intensity at different mangrove sites in Belize had an effect on the heterogeneity of species dominance. Although the patterns in Belize differed from other situations (e.g. Baldwin et al. 2001), it indicated that the effects of large destruction on species diversity also exist for species-poor mangrove systems.

It is as important for species-poor systems as for the others to understand which factors drive species diversity and to assess the role of external perturbations on these factors. The overall objective of the present study is to evaluate the respective importance and interactions of factors influencing species diversity of species-poor systems. We hypothesize that the type of species dominance succession depending on the configuration of interspecific competition and abiotic conditions would determine the system type of response to perturbations, such as hurricanes. In this manner, we evaluate if the intermediate disturbance hypothesis is applicable to mangrove forests and if a general forecast of diversity changes for mangroves subjected to frequent disturbances could be generated. By means of simulation experiments with an individual-based model, we investigated the effects on species diversity of perturbation frequency, perturbation intensity, different abiotic conditions, and interspecific competition.

4.3 Methods

4.3.1 KiWi model general settings

The experiments were carried out with the spatially explicit mangrove model KiWi (Berger & Hildenbrandt 2000 & 2003), developed as dynamic library software written in C++ and using an interface in ©Microsoft ©Visual Basic (DLL and examples available by demand to authors). The KiWi model describes resource competition on the level of individuals and simulated growth of mangrove stands composed of the three main Caribbean species (*Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*). The gap model FORMAN (Chen & Twilley 1998) provided the growth formulas, nutrient and salinity effects multipliers and respective parameters. It is important to note that the KiWi model is not a gap model since it describes trees individually and is spatially explicit. We used Berger and Hildenbrandt (2000) innovation of the Field Of Neighborhood (FON) approach, which simulated inter-individual competition for space and resources. We assumed that the FON described the area where a tree influenced its neighbors and was

influenced by them by sharing limiting resources such as light or nutrient. The FON was defined as a circular intensity field that decreased from the center (stem position) down to the boundary. It specified the intensity of competition exerted by a tree at any position within its neighborhood.

The growth of each individual tree was calculated with the following formula (Berger & Hildenbrandt 2000):

$$\frac{d\text{dbh}}{dt} = \frac{G \times \text{dbh} \times \left(1 - \frac{\text{dbh} \times H}{\text{dbh}_{\text{max}} \times H_{\text{max}}}\right)}{274 + 3 \times b_2 \times \text{dbh} - 4 \times b_3 \times \text{dbh}^2} \times f_s(\text{SALT}) \times f_n(\text{RNA}) \times f_c(F_A) \quad (4.1)$$

where: dbh was the stem diameter at breast height (cm); H was the tree height (cm); dbh_{max} and H_{max} were maximum values of diameter and height for a given tree species (Table 4.1); G , b_2 and b_3 were species-specific growth constants (Table 4.1) and the 3 functions f were growth multipliers. The function $f_s(\text{SALT})$ was the growth multiplier considering the effect of the pore water salinity on growth (Chen & Twilley 1998):

$$f_s(\text{SALT}) = \frac{1}{1 + \exp(d \times (S_{0.5} - S))} \quad (4.2)$$

where: S was the salinity at tree position and $S_{0.5}$ and d were species specific constants (Table 4.1). The function $f_n(\text{RNA})$ was the growth multiplier considering the effect of the relative nutrient availability (RNA) on growth (Chen & Twilley 1998):

$$f_n(\text{RNA}) = c_1 + c_2 \times \text{RNA} + c_3 \times \text{RNA}^2 \quad (4.3)$$

where: c_1 , c_2 and c_3 were species specific constants (Table 4.1). The function $f_c(F_A)$ was the growth multiplier considering the FON effect on growth (Berger & Hildenbrandt 2000):

$$f_c(F_A) = \max \left\{ \begin{array}{l} 0 \quad ; \quad 1 - \varphi \times \left(\frac{1}{A} \sum_{n \neq k} \int_O F_{ON_n}(x, y) dO \right) \end{array} \right\} \quad (4.4)$$

where: φ was an arbitrary maximum value of effect of competition simulating resource sharing capacity, A was the FON area of the focus tree k , n were the neighbors of k , O was the overlap area of the FON areas belonging to the focus and neighbor tree n , and the F_{ON_n} function was returning the intensity of competition of the neighbor n at each point of O . The FON function was calculated as:

$$FON(r) = \left\{ \begin{array}{ll} 1 & \text{for } 0 \leq r < CW/2 \\ \exp\left(-\frac{|\log(F_{\text{min}})|}{R-rbh}\right) \times (r-rbh) & \text{for } rbh \leq r \leq R \\ 0 & \text{for } r > R \end{array} \right\} \quad (4.5)$$

where: rbh was the radius of the stem at breast height of n , r was a distance from the stem position of n , and F_{min} was the minimum intensity of the FON (0.1, Berger & Hildenbrandt 2000) at the FON radius (R). This FON radius (R) depended on the size of the tree:

$$R = a \times rbh^b \quad (4.6)$$

where: a and b were scaling parameters (cf. “setting interspecific competition” and appendix A, page 107). The value of b determined inversely the competition intensity of individuals (Berger & Hildenbrandt 2003).

An overall availability of recruits was considered from simulation data of Chen and Twilley (1998) as $RN_{tot} = 18 \text{ saplings} \cdot 100\text{m}^{-2} \cdot \text{yr}^{-1}$ (Chen & Twilley 1998). However, the annual number of recruits varied randomly and the number from each species (RN_i) was proportionally set according to the occurrence of mature trees (height >5m) of each species:

$$RN_i = \text{int}(rnd_1 \times p_i \times RN_{tot} + rnd_2 \times RN_{tot}) \quad (4.7)$$

where: rnd_1 was a uniform random number between 0.5 and 1.5; rnd_2 a uniform random number between 0.1 and 0.3; and p_i the proportion of mature trees of species i over the total number of mature trees in the plot. The range of variation of the random number in the first term of the bracket (rnd_1) was chosen to describe a natural fluctuation in the availability of recruits per species. The range of variation of the random number in the second term (rnd_2) provided an occasional reappearance of an already excluded species. These recruits were installed randomly on the simulation area, but were removed if the FON intensity (sum of $FON(x, y)$ of all trees at the point of installation x, y) was higher than the species-specific threshold ($F_{A_{max}}$). This threshold was set to $F_{A_{max}} = 0.5$ for *R. mangle* (Berger & Hildenbrandt 2000) and assumed as $F_{A_{max}} = 0.0$ for the two other species to simulate the shade intolerance of seedlings of *L. racemosa* and *A. germinans* (Ball 1980, McKee 1993). Mortality of individual trees not due to external perturbations was growth-rate dependent as described by Berger and Hildenbrandt (2000).

4.3.2 Settings of interspecific competition parameters

The growth parameters (dbh_{max} , H_{max} , G , b_2 and b_3 , Eq. 4.1, Table 4.1) and effects of salinity and nutrient availability (f_s and f_n , Eq 4.2 & 4.3) created species-specific differences in growth response at the stand level. For additional variation in interspecific competition, we considered two ways of simulating spatial competition at the individual level. The first one considered an equal effect of neighboring competition for trees of the same size

Table 4.1: Growth and spatial competition species-specific parameters used in the KiWi model. Sources: (1) Chen and Twilley 1998, (2) see appendix A.

Parameter	Description (Equation, units)	<i>A. germinans</i>	<i>L. racemosa</i>	<i>R. mangle</i>	
dbh_{max}	Maximum diameter at breast height (Eq. 4.1, cm)	140	80	100	(1)
H_{max}	Maximum height (Eq. 4.1, cm)	3500	3000	4000	(1)
G	Growth constant (Eq. 4.1)	162	243	267	(1)
b_2	Constant in height to dbh relationship (Eq. 4.1)	48.04	71.58	77.26	(1)
b_3	Constant in height to dbh relationship (Eq. 4.1)	0.172	0.447	0.396	(1)
d	Salinity effect constant (Eq. 4.2)	-0.18	-0.20	-0.25	(1)
$S_{0.5}$	Salinity effect constant (Eq. 4.2, psu)	72.0	65.0	58.0	(1)
c_1	<i>RNA</i> effect constant (Eq. 4.3)	-0.50	-1.00	0.00	(1)
c_2	<i>RNA</i> effect constant (Eq. 4.3)	2.88	4.42	1.33	(1)
c_3	<i>RNA</i> effect constant (Eq. 4.3)	-1.66	-2.50	-0.72	(1)
a	FON radius scaling parameter for heterospecific competition parameterization (Eq. 4.7)	13.7	17.0	18.0	(2)
b	FON radius scaling parameter for heterospecific competition parameterization (Eq. 4.7)	0.72	0.95	0.83	(2)

for the three species. Thus, they had the same resource sharing tolerance ($\varphi = 2.000$, Berger & Hildenbrandt 2000) and identical a and b parameters (11.0, 0.64, respectively, cf. appendix A, Fig. 4.6). Since the interspecific competition in this parameterization was only through the relative growth rate of each species, it is hereafter referred to as species homogeneous spatial competition. The second parameterization considered that each species had spatially specific competition strength. Particularly, *L. racemosa*, which was described as heliophilic (Wadsworth 1959, Ball 1980, Roth 1992) was set to have a lower sharing tolerance ($\varphi = 2.222$, assuming that the maximum F_A was 10% lower than the other species, i.e. maximum $F_A = 0.45$). Additionally, species-specific a and b parameters (Table 4.1) were used to describe the canopy and root system differences for the three species. These parameters were tuned (Appendix A, Fig 4.6) to reproduce field data of monospecific stands of tree size vs. density relationships from Belizean offshore mangroves, and to set *L. racemosa* as less competitive than the two other species. This lower competition capacity of *L. racemosa* was until diameter at breast height (dbh) < 80 cm; while the a and b values also determined that *A. germinans* was more competitive than *R. mangle* until $dbh > 20$ cm. This second parameterization is hereafter referred to as species heterogeneous spatial competition.

4.3.3 Effects of abiotic conditions

Our first exercise was set to analyze the effect of abiotic conditions on species diversity without any perturbations. We also investigated the effect of interspecific competition on species dominance succession in this exercise. Five salinities (0, 20, 40, 50 and 60 psu) and four relative nutrient availabilities (RNA) (100%, 80%, 60% and 40%) were considered. Ten replicates of all possible salinity/ RNA scenarios on the two competition parameterizations were simulated on a 6000m² plots and during 1000 years.

The number of trees and basal area per species were used to calculate relative abundance and dominance for each time step and transformed into importance values (IV) according to Cintrón and Novelli (1984):

$$IV_i = \frac{100 \times Dens_i}{\sum_{j=1}^q Dens_j} + \frac{100 \times BA_i}{\sum_{j=1}^q BA_j} \quad (4.8)$$

where: IV_i , BA_i and $Dens_i$ were the importance values, basal area and density of trees of the species i and q was the number of species. As a measure of species diversity, we used the index of species dominance heterogeneity (I_{SDH}) from Piou et al. (2006). It was adapted from the reciprocal index

of Simpson (Hill 1973) and computed as follows:

$$I_{SDH} = \frac{\sum_{i=1}^q IV_i \times (\sum_{i=1}^q IV_i - 1)}{\sum_{i=1}^q (IV_i \times (IV_i - 1))} \quad (4.9)$$

This index indicated relative species dominance in our three-species system and would be given value of 0 if no trees could grow at all because of harsh abiotic settings. If trees could grow, the I_{SDH} would take value from 1 (only 1 species present on the plot) to 3 (the 3 species representing each 33% of importance on the plot). It was not mathematically independent from species richness; therefore, we decided not to use the term “evenness” to avoid confusion with its calculations in community studies (Smith & Wilson 1996). However, through the variation of relative species dominance this index could indicate if different three-species configurations of our system were relatively rich or not in term of species diversity. As indicators of salinity/*RNA* effect on species diversity, the median, 1st and 3rd quartiles of I_{SDH} for each scenario over the last 400 yr of simulations were calculated.

4.3.4 Effects of perturbation regimes

The second exercise was set to analyze the effects of perturbation regimes on species diversity. Massive killing events, which simulated mortality induced by a tropical storm or hurricane, were applied at different mortality rates (intensity) and frequencies. Because there is inconsistency in the literature on the way authors described storm resistance capacity according to species or tree size (e.g., Vermeer 1963, Stoddart 1963, Bardsley 1984, Roth 1992, Smith et al. 1994, Roth 1997, Imbert et al. 1998, Sherman & Fahey 2001, Baldwin et al. 2001, Imbert 2002), we could not considered the mortality events related to size or species in our simulations. The applied intensities were probabilities of 30%, 50%, 70%, 90% and 99% of mortality for each tree at the event times. The perturbation frequencies (1/100yr, 1/80yr, 1/60yr, 1/40yr, 1/20yr and 1/10yr) determined the exact number of years between two events.

To achieve a stabilized system in term of number of trees, we excluded the first 400 simulation years. Perturbations were applied only on the following 400 yr so that the total simulated time was 800 yr. The role of abiotic conditions on system response to perturbation was considered by selecting scenarios from the results of the previous exercise. Benign (salinity 0 psu and 100% *RNA*) and medium (salinity 50 psu and 80% *RNA*) conditions were analyzed but extreme ones were not considered because they resulted in a system overwhelmed by one species. Ten replicates were simulated for

each abiotic scenario (benign or medium), considering each competition parameterization (homogeneous or heterogeneous spatial competition) and all mortality rate/perturbation frequency scenarios. Similar to the previous exercise, the median of I_{SDH} was calculated over the last 400 yr for all cases. To analyze the significance of perturbation intensity with selected perturbation frequency, Kruskal-Wallis non-parametric analysis of variance (ANOVA) by ranks were applied on the last I_{SDH} values of each simulation. To analyze the effect of perturbation frequency with selected perturbation intensity, identical non-parametric ANOVA's were done considering all the I_{SDH} values of the simulated perturbation time. Mann-Whitney U tests were used to assess significant differences of extremes and intermediate I_{SDH} values in order to validate disturbance effect patterns such as U-shaped, linear increase or decrease, irregular or bell-shaped.

4.4 Results

4.4.1 First exercise: effects of abiotic conditions

Extremely low relative nutrient availabilities (40% *RNA*) and extremely high salinities (60 psu) decreased significantly the index of species dominance heterogeneity (I_{SDH}) for both spatial competition parameterizations (Fig. 4.1). These extreme abiotic conditions caused species exclusion through the parameterization of *R. mangle* and *A. germinans* growth characteristics to be non-adapted to high salinities and low nutrient availabilities respectively. At the worst condition (salinity 60 psu and 40% *RNA*), no species grew at all, resulting in $I_{SDH} = 0$. Considering the rest of the abiotic scenarios, highest I_{SDH} values in both spatial competition parameterizations were found at intermediate levels of salinity and *RNA*. The median I_{SDH} values over the last 400yr were relatively similar between the two spatial competition parameterizations. However, I_{SDH} values and species importance varied more importantly during the first 400yr for all abiotic scenarios. For a medium case of abiotic scenario (salinity 50 psu and 80% *RNA*), variations of species importance values showed a cycling of species dominance (Fig. 4.2). The species heterogeneous spatial competition parameterization created a quick succession from *L. racemosa* to *A. germinans* (Fig. 4.2b) during the first 50yr of simulations. With homogeneous spatial competition, the dominance of *L. racemosa* varied but stayed always higher than the two other species (Fig. 4.2a). Identically, for benign abiotic scenarios, the species heterogeneous spatial competition created species succession, while the homogeneous spatial competition showed importance values variation without

shift of species dominating.

4.4.2 Second exercise: effects of perturbation regimes

For the analysis of phenomena explaining the response pattern, we concentrated only on the medium abiotic scenario. Massive mortality altered the temporal dynamic of I_{SDH} (Fig. 4.3). The low perturbation regime (Fig. 4.3a) did not modify the general trend of variation of species importance values and I_{SDH} compared to non-disturbed dynamics (Fig. 4.2b). With an intermediate perturbation regime (more frequent and stronger disturbances, Fig. 4.3b compared to 4.3a) *L. racemosa* gained in importance although still less important than the two other species. This reduced the difference in relative importance of the three species and thus led to an overall higher I_{SDH} than with the low perturbation regime. The most frequent and destructive perturbation regime (Fig. 4.3c) switched the system quickly from *A. germinans* to *L. racemosa* dominance. At this level of perturbation regime, each disturbance had an effect of keeping *L. racemosa* as the most important species on the plot. This corresponds to the original succession situation at beginning (first 10yrs) of simulations, as if *L. racemosa* was the pioneer

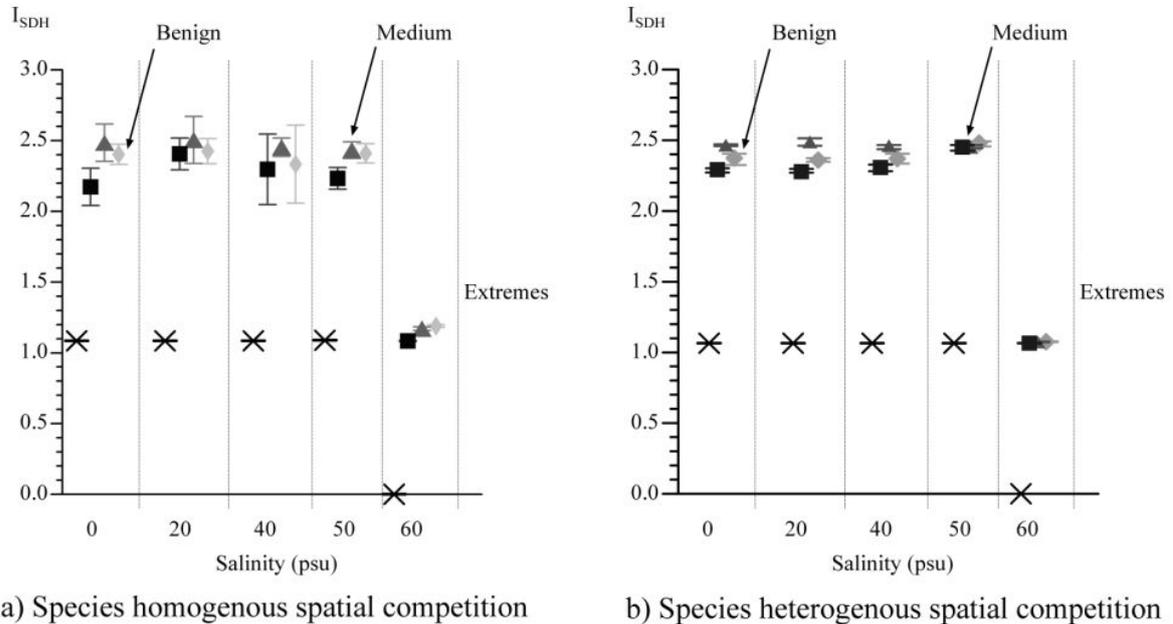


Figure 4.1: I_{SDH} variations according to salinity and relative nutrient availability (RNA : diamond=100%, triangle=80%, square=60%, cross=40%) conditions for the two competition parameterizations. Points are median values of replicate simulations, error bars represent first and third quartiles.

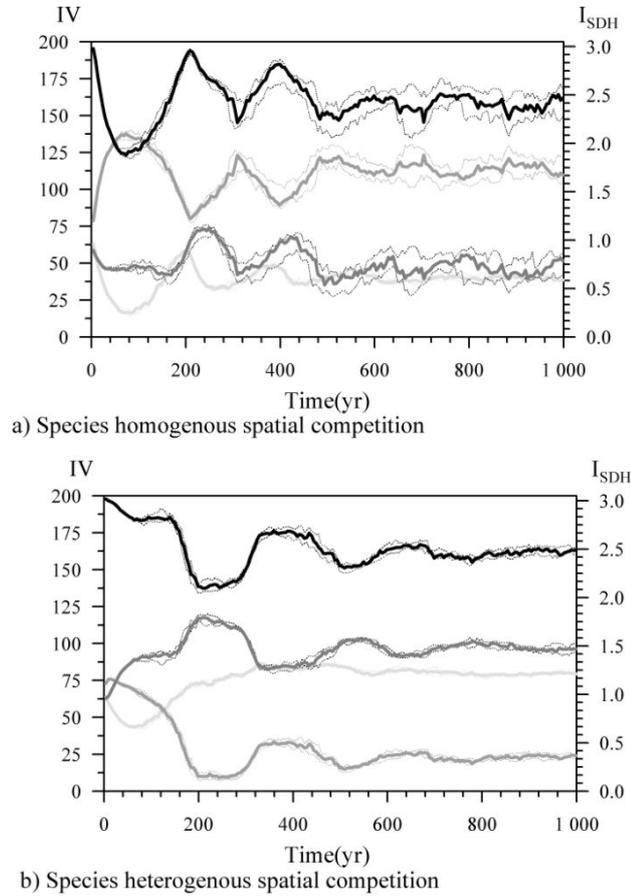


Figure 4.2: Dynamical variations of the two competition parameterizations with selected abiotic scenarios (medium= Salinity 50psu and RNA 80%) in species relative importance and I_{SDH} (Black line = median I_{SDH} , dark grey = median importance values (IV) of *Avicennia germinans*, grey = median IV of *Laguncularia racemosa*, light grey = median IV of *Rhizophora mangle*, dash lines = respective first and third quartiles)

species of the system. However, this change of dominance did not modify significantly the I_{SDH} values compared to low or absent perturbations because the ratios of species importance values were conserved. In this case, the high frequencies stabilized these ratios and I_{SDH} values over time.

Variations in perturbation regimes always had an effect on the species dominance heterogeneity of the simulated stands (Fig. 4.4). However, the overall patterns of simulation results depended on the different competition parameterization. The species homogeneous spatial competition parameterization (Fig. 4.4a) showed lower I_{SDH} values at intermediate perturbation regimes than at lower and higher perturbation frequencies and intensities. This U-shaped curve pattern was clearly observable for the influence of fre-

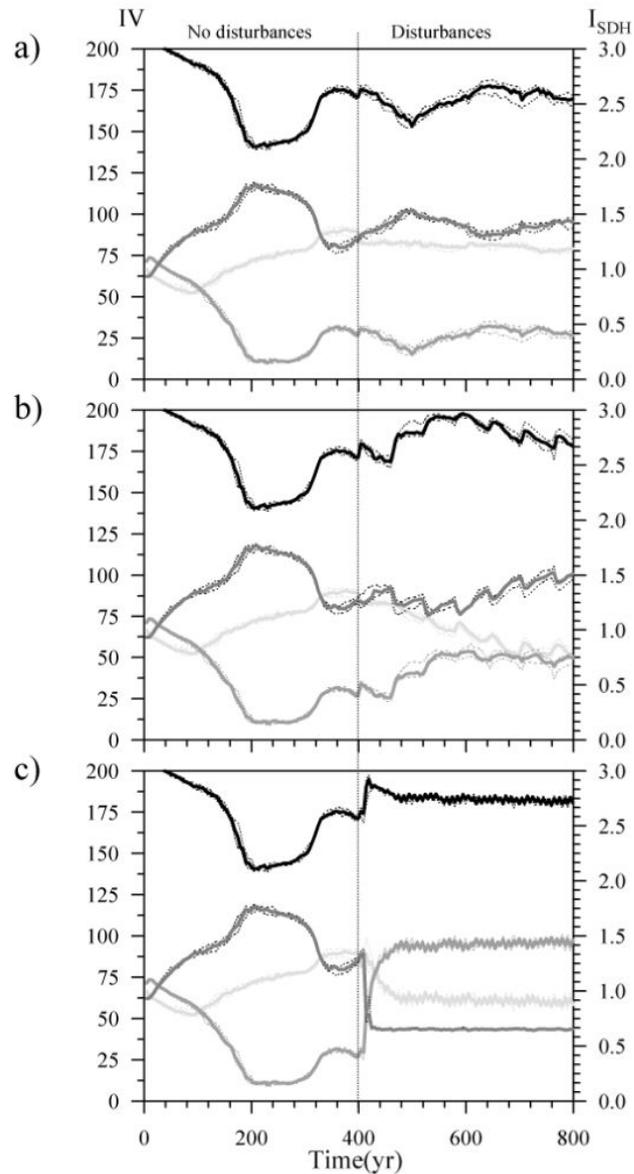


Figure 4.3: Dynamical variations in species relative importance and I_{SDH} for the heterospecific competition parameterization and medium case of abiotic scenario (salinity 50psu, 80% RNA), and perturbation regimes (a: frequency= 1/100yr, intensity= 30% mortality; b: frequency= 1/60yr, intensity= 70% mortality; c: frequency= 1/10yr, intensity= 99% mortality). (Black line = median I_{SDH} , dark grey = median importance values (IV) of *Avicennia germinans*, grey = median IV of *Laguncularia racemosa*, light grey = median IV of *Rhizophora mangle*, dash lines = respective first and third quartile)

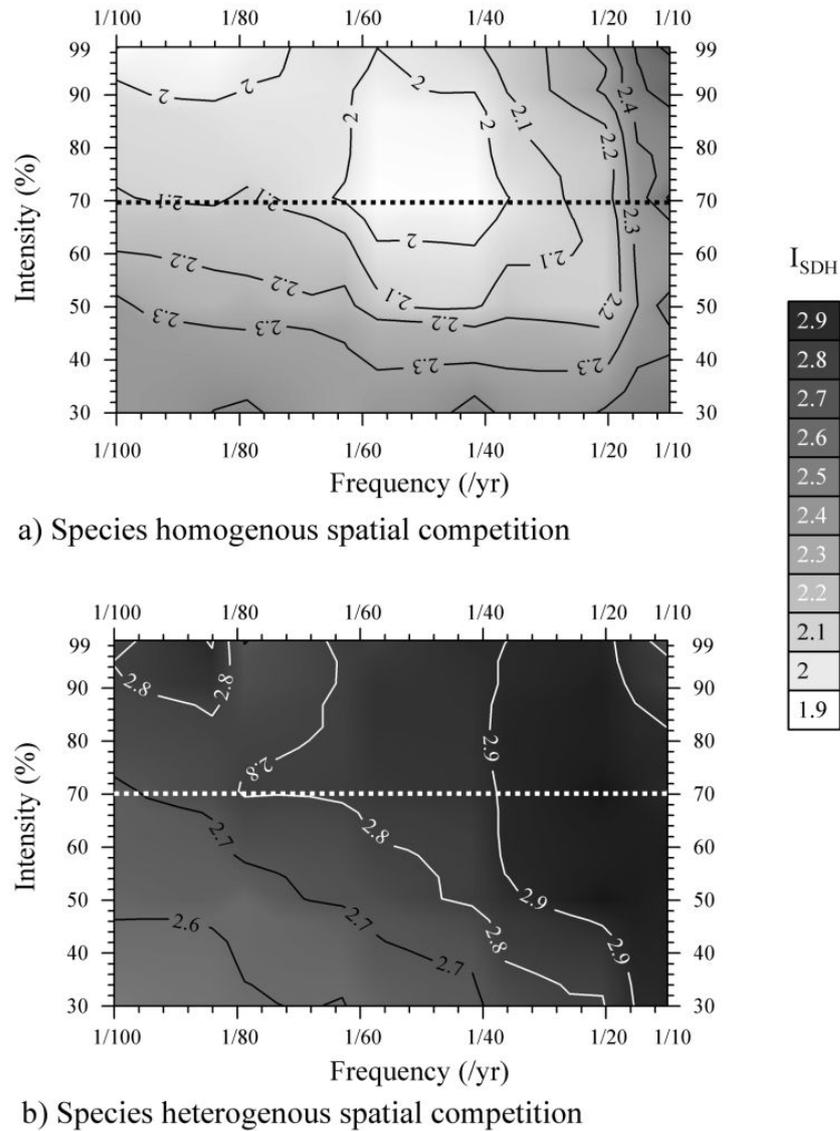


Figure 4.4: Median I_{SDH} variations according to perturbation frequency and intensity for the two competition parameterizations (a and b) with medium abiotic scenario (Salinity 50psu and 80%RNA). Dashed lines represent selected pattern illustration for figure 4.5.

quency regime with a selected perturbation intensity (Fig. 4.5a), although the values showed high variation among simulations (1st and 3rd quartile variations). The species heterogeneous spatial competition parameterization resulted in an overall increase in I_{SDH} values with increasing disturbance regimes until non-extreme intensity and frequency, followed then by a small decrease (Fig. 4.4b). Thus, this trend led to an overall bell-shaped pat-

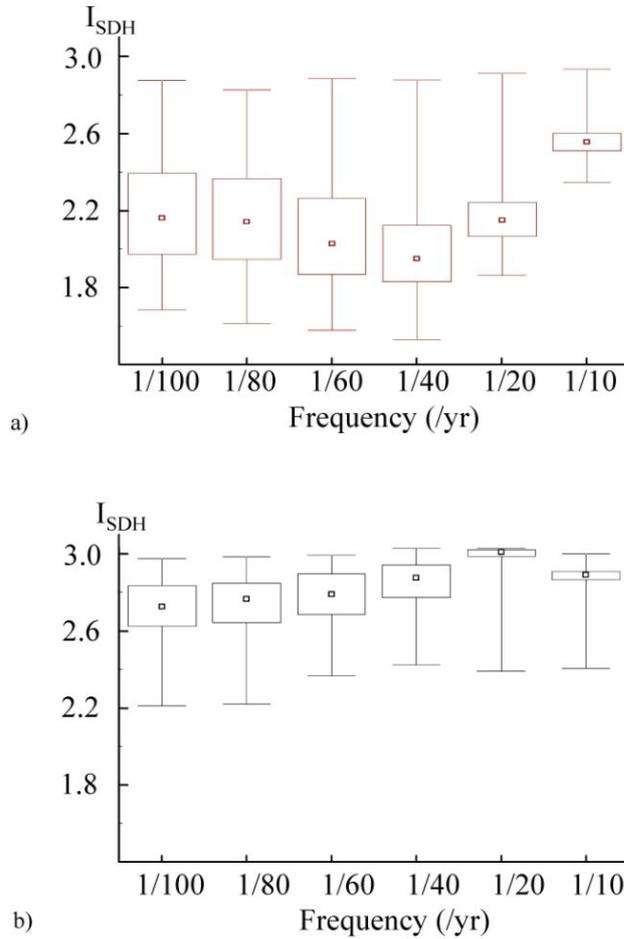


Figure 4.5: Median I_{SDH} variations following perturbation frequency for the two competition parameterizations (a and b) with selected mortality intensity (70%) and medium abiotic scenario (Salinity 50 and RNA 80) ($N=30$ for each point, boxes represent first and third quartiles, error bars represent minimum and maximum).

tern, which was also more visible for the influence of frequency regime with selected perturbation intensity (Fig. 4.5b).

Figure 4.5 shows two examples of possible I_{SDH} variation pattern for medium abiotic conditions. These types of pattern were analyzed for benign and medium abiotic conditions and for both spatial competition scenarios. Overall, we found a clear difference of patterns between the two spatial competition parameterizations. The homogeneous spatial competition parameterization led to some cases of U-shaped patterns while the heterogeneous spatial competition on the contrary showed bell-shaped patterns. Not all perturbation regimes led to these U- or bell- shaped patterns: some led to

linear increasing or decreasing patterns, or non-significant or irregular patterns. These trends were respected with the two selected abiotic conditions (see Appendix B, page 110 for detailed results).

4.5 Discussion

This study illustrated that even for species-poor systems, the dynamics and the processes which could explain variations in species diversity are diverse and interconnected. The interplay of abiotic conditions and interspecific competition produces a set of potential vegetation dynamics. Depending on the perturbation regime, a system will follow a particular trajectory of this set, and thus eventually show or not the expected intermediate disturbance hypothesis pattern.

Our simulations integrate the actual knowledge on Caribbean mangrove species of species-specific parameterization of growth, adaptations to abiotic conditions, settlement and spatial competitive strength. The results of the first exercise illustrate that abiotic conditions influence the dominance distribution of these species, up to eventually excluding one or more species. On the contrary, intermediate conditions of pore water salinity and nutrient availability favorable to all three species lead to higher coexistence. The setting of species-specific growth parameters of our model is thus able to re-create the diversity of species dominance observed in the Caribbean. Other factors that were not considered in this study, such as tidal regime, temperature, soil physico-chemical properties (e.g., redox potential or sulfide contents), could have similar effects on species richness and dominance in mangrove systems (Ball 1980, McKee 1993).

The results of the first exercise also show that changes in the characteristics of species-specific spatial competition do not modify significantly the overall measure of species diversity. However, at a given abiotic condition, a change in the settings for spatial competition drastically alters the temporal variations of relative species dominance. Our parameterization of homogeneous spatial competition leads to a cycling dynamic but with *L. racemosa* dominating all the time because of its faster growth rate. The hypothesis behind this parameterization is that species differ in their resource use capacity but not in a spatially explicit way. For example, trees of the same size would have the same spatial extent of resource use disregarding their species. In contrast, the heterogeneous spatial competition parameterization is derived from the hypothesis that individuals of *L. racemosa* are less competitive for spatially distributed resources than individuals of other species (Wadsworth 1959, Ball 1980, Roth 1992). The reduction of resource-sharing tolerance

for the *L. racemosa* trees increased the effects of neighbors on their growth rates. Additionally, species-specific changes in the FON radius influenced species interactions by conferring lower competitive strength to *L. racemosa* individuals than equal-sized *A. germinans* or *R. mangle* trees. Thus, after the first years of fast growth of *L. racemosa* trees this heterogeneous spatial competition parameterization produced a shift in dominance. Thus, this succession resulted from the switch in the importance of two forces: a) the primary growth rate of *L. racemosa* which is known to be faster than for the other species under low salinity conditions, high nutrient and light availability (McKee 1995, Sherman et al. 1998, Lovelock & Feller 2003), and b) the low strength of spatial interspecific competition of *L. racemosa* (as hypothesized by Berger et al. 2006). These characteristics are typical of pioneer-like species in any plant system. In mangrove forests, such successions were described in some secondary recovery areas (Ball 1980, Berger et al. 2006), which suggests that our second spatial competition parameterization is supported by some field observations. These differences in the dynamics between the two parameterizations become especially important when considering the effects of perturbations.

The simulations with perturbations illustrated that species dominance of our system depended on the frequency of the destruction events and their intensities. However, we have seen that the pattern of response changed mainly depending on the competition parameterization and thereby the successional dynamic. Perturbations created gaps that would take the same trajectory as the system's dynamics observed without perturbations. For each gap recovery, the seedlings availability depended on the dominant species in the rest of the stand. In the case of homogeneous spatial competition parameterization, if the system was perturbed each time when the majority of gaps were in the cycling phase of highest dominance of *L. racemosa*, the dominance of this species would increase more and more, as in a resonance phenomenon. This situation was created at intermediate perturbations regimes, leading to the lowest I_{SDH} values. With extreme disturbance regime, the system would achieve the cycling phases earlier and, thus, would return to a more even species distribution. This scenario led to higher I_{SDH} values, and overall created the observed U-shaped patterns. With the heterogeneous spatial competition parameterization, perturbations caused the system to return iteratively to conditions seen during the initial succession phases. Since *L. racemosa* was the most pioneer-like of the three species, it obtained higher importance with stronger and more frequent perturbations, which created a more homogeneous species dominance. Eventually, with extreme perturbation regimes, *L. racemosa* dominated completely, reducing the index of species dominance heterogeneity. In mangrove forests, it is therefore possible

to observe the bell-shaped pattern typically described by the intermediate disturbance hypothesis (IDH) (Connell 1978) if we have a biotic configuration where *L. racemosa* is pioneer and succession happens during stand recovery or establishment. However, in addition to bell-shaped or U-shaped patterns, our results also revealed many cases of linear increases or decreases due to perturbation regimes not fitting exactly the resonance of the recovery dynamics.

This diversity of responses to perturbation fits the observations of Mackey and Currie (2001) and the prediction of the IDH axioms detailed by Sheil and Burslem (2003). Specifically, to have an IDH pattern you need: a) a dominance successional sequence when no perturbations occur, b) succession due to competitive exclusion of fastest growing trees, and c) perturbations bring the system back to earlier successional stages. The results of our individual-based model simulating competition at individual-level confirm these axioms. The homogeneous competition parameterization of our study did not create succession and therefore did not exhibit a pattern predicted by the IDH. However, this dynamic is possible in nature (e.g. in understory species systems as in Beckage & Stout 2000) and in mangrove ecosystems particularly. Only few studies have observed a real species succession in mangrove forests (e.g. Ball 1980, Berger et al. 2006). Lugo (1980) concluded that zonation was a steady state result of abiotic conditions and refuted Davis' (1940) hypothesis that zonation was the result of succession and land building processes. Since Lugo's paper, succession in mangroves has been cautiously attributed to changes in abiotic conditions because of external factors, but rarely to species-induced modifications of abiotic conditions (e.g. Bertrand 1999). Because the IDH pattern is the expression of the dynamics of species succession, it can be used to compare species succession at different disturbance levels, or conversely, to compare the recovery dynamics of sites that exhibit different succession dynamics. Both aspects have never been considered in mangrove ecology. Such studies could support our simulation results that in some cases succession could be due to plant-plant interactions and not always exclusively to abiotic conditions changes.

Finally, our study at the individual-level demonstrates that even if abiotic conditions strongly influence species composition in mangrove forests, spatial plant-plant interactions also play an important role. We showed that the successional dynamic is dependent on the capacities of individuals of different species to compete spatially for resources, and that these dynamic determine the way species diversity will increase or decrease in case of perturbations. Thus, we demonstrate that variations of mangrove species diversity due to perturbation regime will depend on a series of interacting factors: succession configuration, actual dynamic phases, plant spatial interactions and abiotic

settings. Additionally, field studies show that changes of abiotic settings after perturbations (e.g., Cahoon et al. 2003), recruitment patterns (e.g., Baldwin et al. 2001, Clarke 2004, Piou et al. 2006) and also differences of resistance of species to the considered perturbations (Baldwin et al. 2001, Imbert 2002) could influence species composition of mangroves. Hence, forecasting a general trend of evolution of species diversity of mangrove forests only considering the perturbation regime seems risky. It could be possible only in a site-specific case, knowing for this site not only the abiotic conditions, but also the type of species interactions and succession phenomenon that could occur.

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4.8 Appendices

4.8.1 Appendix A

In the KiWi model, the FON radius R of a tree depends on its size:

$$R = a \times rbh^b \quad (4.10)$$

where: a and b are scaling parameters. The parameterization of a and b can be effectuated from the dbh -density trajectories of a self-thinning phenomenon.

Demonstration:

In equation 4.10, the rbh is half the dbh , so 4.10 can be written:

$$R = a \times \frac{1}{2^b} \times dbh^b \quad (4.11)$$

The FON approach has been seen as reproducing the self-thinning trajectory very well (Berger and Hildenbrandt 2003). During the self-thinning in KiWi model, because of the mortality function, the total FON area of all individuals can be considered as constant since the dead individuals are replaced by growth of the remnant. This corresponds to a constant maximum resource use. Let assume this constant total area be FON_{tot} . We could simplify its calculation as:

$$FON_{tot} = N \times FON_{ind} \quad (4.12)$$

where FON_{ind} is the mean area of the FON area of the individuals defined as:

$$FON_{ind} = \pi \times R^2 = \pi \times a^2 \times \frac{1}{2^{2b}} \times dbh^{2b} \quad (4.13)$$

where R and dbh are respective mean values assuming they represent the entire community. Assuming that during self-thinning we have the relationship of the dbh -density trajectory:

$$\begin{aligned} \log(N) &= \alpha + \beta \times \log(dbh) \\ \text{or } N &= \exp(\alpha) + dbh^\beta \end{aligned} \quad (4.14)$$

Interchanging Equation 4.13 in 4.12 and comparing to 4.15 we get:

$$N = \exp(\alpha) + dbh^\beta = \frac{FON_{tot}}{FON_{ind}} = FON_{tot} \times \left(\frac{2^{2b}}{\pi \times a^2} \right) \times dbh^{-2b} \quad (4.15)$$

Since $\exp(\alpha)$ and $FON_{tot} \times \left(\frac{2^{2b}}{\pi \times a^2} \right)$ are not dependents on dbh , we can link the β parameter directly to the FON b parameter:

$$\beta = -2b \quad (4.16)$$

Identically we can derive the value of a :

$$a = \sqrt{\frac{2^{2b} \times FON_{tot}}{\pi \times \exp(\alpha)}} \quad (4.17)$$

We determined with the KiWi model that FON_{tot} is constant $\sim 215\%$ and not depending on a nor b . These relationships are confirmed by simulation experiments with monospecific stands (Fig. 4.6).

Parameterization of species-specific values

Data from monospecific stands of Belizean mangroves (I.C. Feller, F. Chi and C. Piou unpublished) at different density were used to create regressions among *dbh* and density. This gave us the α and β parameters and therefore allows us to calculate (with equations 4.16 and 4.17) the parameters a and b for *Rhizophora mangle* and *Avicennia germinans*. Figure 4.6 shows the field data, the linear regressions and results of monospecific simulation without recruitment with the corresponding FON a and b .

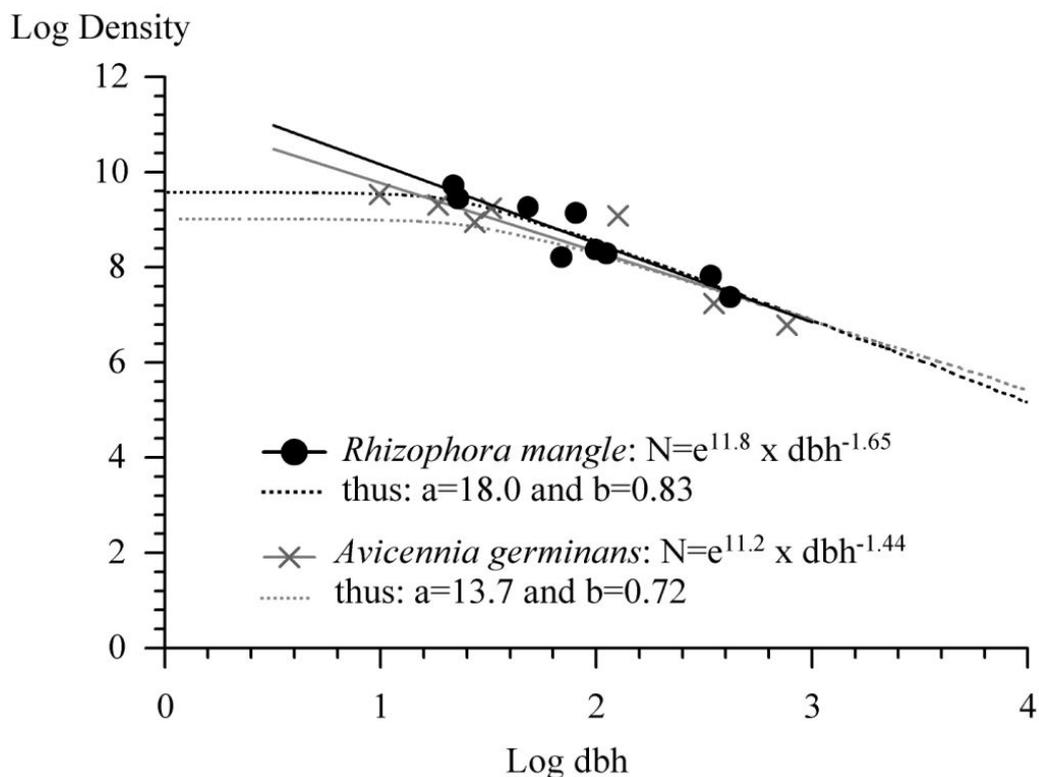


Figure 4.6: Field *dbh*-density (cm and stem/ha) data on natural logarithmic scale with corresponding linear regression (plain lines) and simulation results (dashed lines) of monospecific stand of *Rhizophora mangle* (black) and *Avicennia germinans* (grey) without recruitment.

For *Laguncularia racemosa*, not enough monospecific field data were available, so we estimated that this species was less competitive in Belize in term of spatially distributed resource such as light. This was then considered in the a and b parameter giving a bigger b value (0.95) and smaller a (17.0) value than for *R. mangle*.

Parameterization of species-identical values

To use the same approach for the tuning of the a and b parameter in the first parameterization (species homogeneous spatial competition), data of density and mean diameter from mixed stands of the three species were considered. We used the data from plots of the CARICOMP program (CARICOMP 2002, http://www.ccdc.org.jm/mangrove_data.html) over the entire Caribbean region to create the regression and calculate the parameters a and b considering all three species (Fig. 4.7).

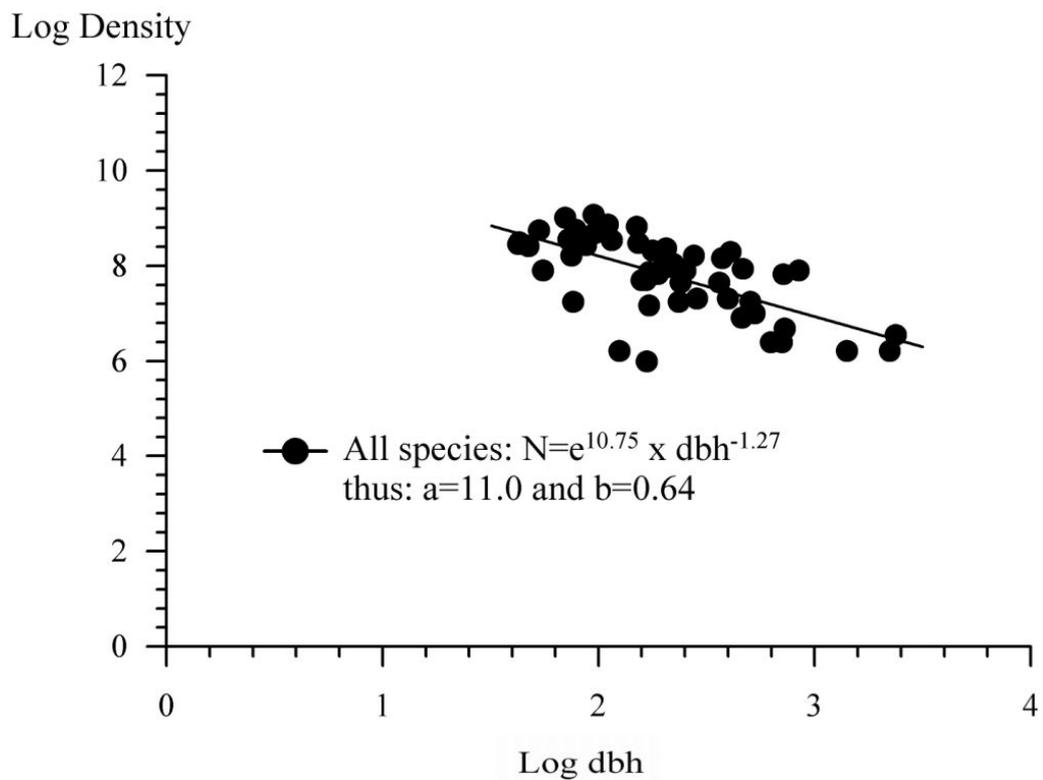


Figure 4.7: CARICOMP dbh -density (cm and stem/ha) data of mixed forests on natural logarithmic scale with corresponding linear regression (plain line).

4.8.2 Appendix B

The analysis of variations in species diversity (I_{SDH}) of the system depending on the perturbation regime showed different type of patterns for the different parameterizations (Fig. 4.8). The homogeneous spatial competition parameterization with benign abiotic conditions led to 4 U-shaped patterns out of 11 analyses. The heterogeneous spatial competition parameterization with

benign abiotic conditions led to 4 bell-shaped patterns out of 11 analyses. In both cases, the rest of the analyses showed irregular, increasing or decreasing pattern of I_{SDH} variations. With medium abiotic conditions the patterns were more often U-shaped or bell-shaped, but with an identical trend: the homogeneous spatial competition parameterization led to 6 U-shaped patterns and the heterogeneous spatial competition led to 7 bell-shaped patterns out of 11 analyses in both cases.

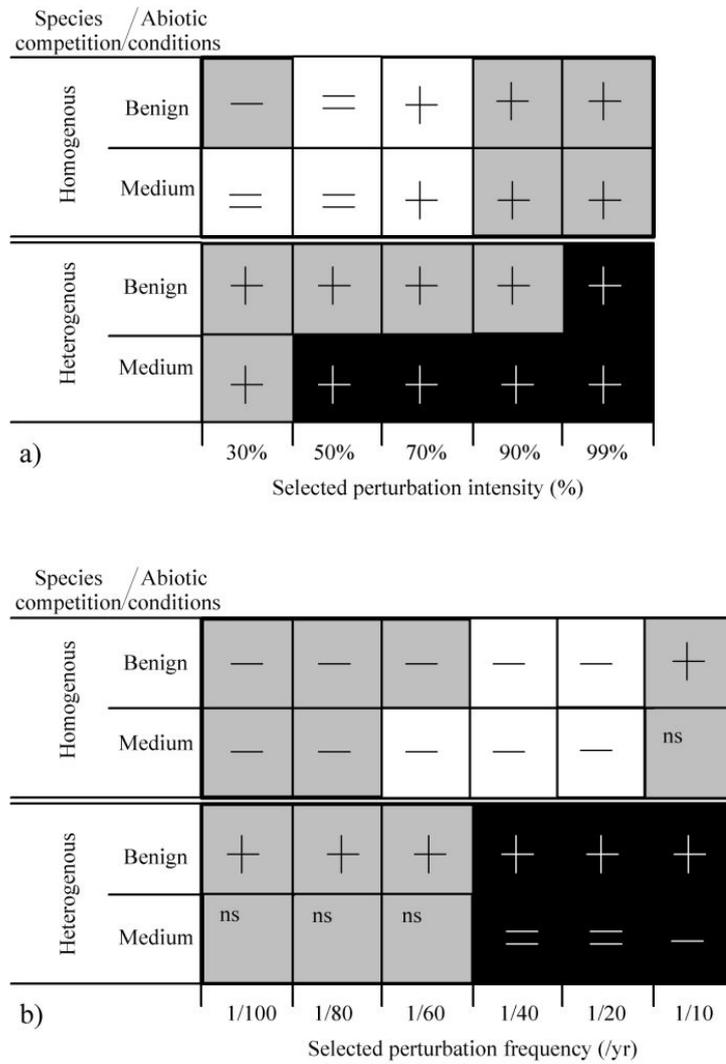


Figure 4.8: Patterns of system response in median I_{SDH} variations according to frequency effect with selected intensity of disturbance (a) or according to intensity effect with selected frequency of disturbance (b). White boxes indicate U-shaped pattern of response, grey boxes indicate linear increase/decrease or irregular pattern of response, black boxes indicate bell-shaped pattern of response. +, - and = show respectively significant increase, decrease or no differences of I_{SDH} values from start to end of pattern.

Chapter 5

Importance of abiotic gradients on mangrove zonation patterns: a simulation experiment



Importance of abiotic gradients on mangrove zonation patterns: a simulation experiment

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Article in preparation

5.1 Abstract

Species zonation patterns are among the most studied features of mangrove ecology. Many hypotheses of forest dynamic processes are proposed to explain these patterns. However, the time and spatial scale at which these processes happen make that experiments are difficult to establish to verify these hypotheses in the field. Individual-based models trying to reproduce zonation patterns could help in the assessment of these hypotheses. The objective of this study was to evaluate the importance of the effect of different abiotic gradients on species zonation in 4 mangrove sites around Calabash Cay, Belize. We used the spatially explicit individual based model KiWi to simulate the growth of Caribbean mangrove trees. We tested if the patterns of basal area of each species were better reproduced with or without the influence of: a salinity and/or nutrient gradient influencing the growth of individuals, and a tidal gradient limiting the establishment of recruits along the sites. The pattern-oriented modeling information criterion was applied to evaluate the capacity of each scenario to reproduce the patterns. The results showed an apparent role of tidal effect on the two eastern sites of Calabash. The salinity or nutrient gradients were necessary to reproduce the zonation of the western sites. These results also implied the importance of seedlings availability and past history in the recovery of mangrove zonation patterns. Further modeling studies should assess additional processes at various spatial and temporal scales to analyze the relative importance of all the proposed hypotheses explaining the mangrove species zonation patterns.

Key words: Mangrove zonation hypotheses, individual-based modeling, pattern-oriented modeling, information criterion

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5.2 Introduction

Mangrove forests are distributed along tropical and sub-tropical coastlines and estuaries. Although these ecosystems are constituted by a low number of tree species compared to other tropical forests, mangroves present a high diversity of structures. Several classifications of these structures exist and environmental settings are often believed to drive them (e.g. Tomlinson 1989, Smith 1992, Saenger 2002). Among these structural patterns, horizontal zonation across the intertidal area has been subject to a plethora of work and hypotheses (review by Smith 1992 and Saenger 2002). Such patterns distinguish between structural characteristics (structural zonation) and species dominance (species zonation), both described as bands often parallel to the shore. The structurally defined zones differ in tree density, canopy height or tree diameters while the species defined zones have different species composition. The hypotheses proposed to influence the species zonation patterns are so far: *H1*) plant succession associated to land building (Davis 1940, Bertrand 1999), *H2*) geomorphological factors (Thom 1967), *H3*) differential dispersal of propagules due to tidal gradients (Rabinovitz 1978) or predation gradients (Smith 1987), *H4*) species-specific physiological adaptations to physico-chemical gradients (Macnae 1968), *H5*) spatial interspecific competition at individual tree level with or without habitat partitioning (Ball 1980, Clarke 2004), *H6*) perturbation regime (Piou et al. 2006(Chapter 3), Imai et al. 2006). Land building with plant succession and geomorphological factors are intertwined in their effect on the installation or modification of the zonation pattern (Saenger 2002) and are typically acting at large spatio-temporal scales. Smith (1992) argued after Lugo (1980) that land-building is not at the origin of zonation patterns, and that the geomorphological factors are directly influencing the primary succession and zonation. Spatial interspecific competition implies interaction among individuals. Many different species-specific characteristics at the individual level influence these interactions: growth capacities according to abiotic/biotic conditions, seedling shade or other stress tolerance, seed production and establishment. The effect of spatial interspecific competition on zonation is therefore related to hypotheses concerning the effect of biotic and abiotic gradients, as well as the capacity of the species to cope with perturbations at small scale. All these hypotheses of influencing factors are summarized in figure 5.1 depending on their spatio-temporal scale of influence (vertical position and extent of box) and their initiator or modifying/sustaining roles (horizontal position

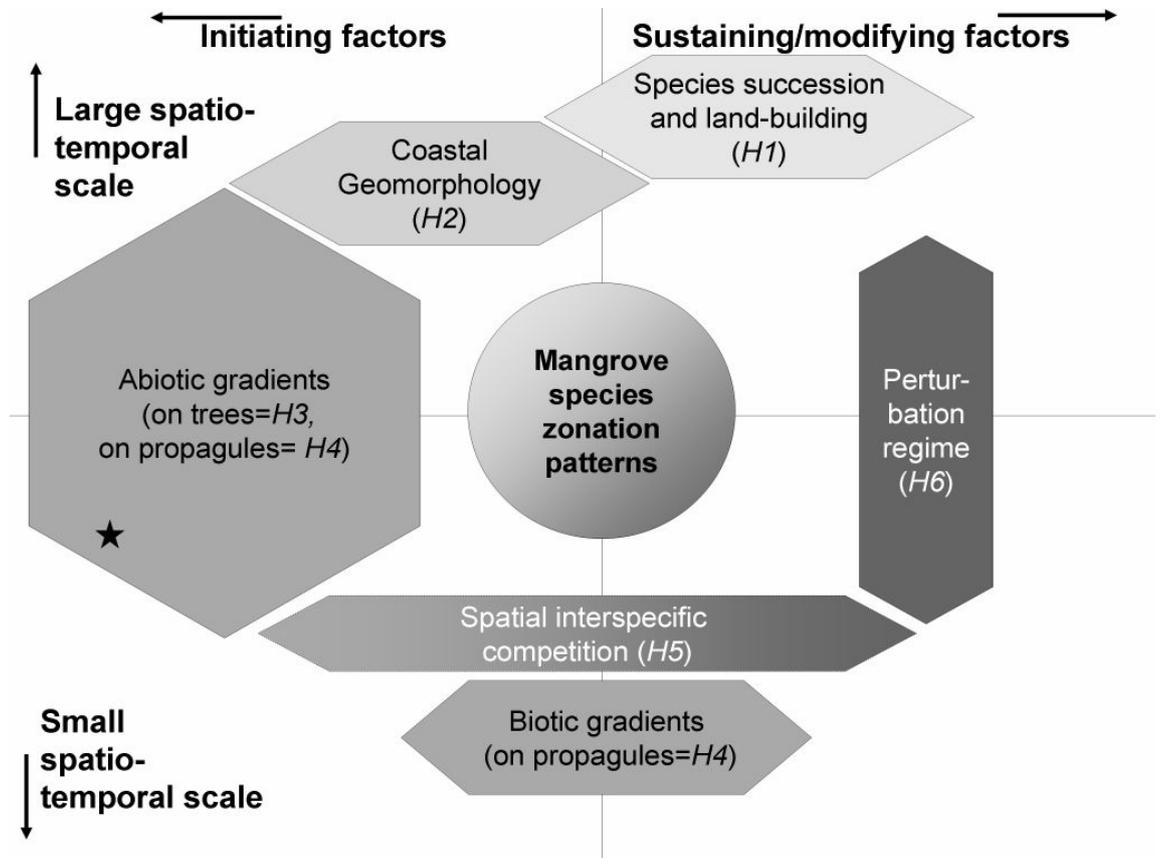


Figure 5.1: Scheme of repartition of the hypotheses of factors affecting mangrove species zonation patterns according to their capacity to be at the origin of zonation patterns or to influence on them (horizontally), according to the scale of their impact (vertically) and according to their interactions (proximity of the boxes). In parenthesis are the hypothesis number referred to in text. The star shows the focus of this study assuming spatial interspecific competition.

and extent of box). Additionally, the strength of connections between these factors is indicated by the proximity of boxes.

Until now the study of species zonation patterns and related hypotheses was limited to static descriptions or short-term temporal analyses (e.g. Bertrand 1999, McKee 1995b, Piou et al. 2006 (Chapter 3)) at the community level, or to experiments on individual tree performance by modification of environmental conditions (e.g. McKee 1995a,b,c) at the individual level to generalize at the community level. The actual processes acting at the individual level and proposed to explain the patterns at system level should be tested but temporal and spatial scale problems obviously limit such experiments on the field. The advantage of individual-based modeling using a

pattern-oriented approach is the capacity to simulate different assumptions about individual species-dependent characteristics in order to assess their reliability. In reproducing the patterns observed in nature and particularly emergent properties (Breckling et al. 2005) such as zonation pattern, the pattern-oriented approach gives the possibility to make inference on processes more likely to occur (e.g. Wiegand et al. 2003, Grimm et al. 2005).

Individual based modeling in mangrove ecology started with a gap model by Chen and Twilley (1998). Their model (FORMAN) reproduced basal area values and was used as prediction tool of species dominance changes of Floridian mangroves (Chen and Twilley 1998) and for prediction of regeneration management of the Ciénaga Grande de Santa Marta (Twilley et al. 1999). The FORMAN model incorporated interspecific competition with species-specific growth constants. The spatial competition was assumed to happen only for the light resource. It was evaluated through relationships among leaf-area index and size of the trees, assuming a maximum leaf-area per gaps. Berger and Hildenbrandt (2000) proposed to simulate the competition for spatially distributed resources at the individual level with the Field Of Neighborhood approach (FON), in the so-called KiWi model. The FON approach does not specify the types of resources competed for. Instead, it assumes that the effects of competition for spatially distributed resources can be synthesized all together into one variable. The KiWi model produced a set of theoretical (Berger and Hildenbrandt 2000, 2003, Berger et al. 2002, 2004, Bauer et al. 2002, 2004, Chapter 4) and a pattern-oriented study (Berger et al. 2006). Nevertheless, the application of these models was so far not focusing on zonation patterns. The species zonation pattern is one of the most studied aspects of mangrove ecology. Thus, it should definitely be tested with simulations having diverse parameterization corresponding to different hypotheses to analyze the reliability and the importance of each of them.

The objective of this study is to evaluate the importance of the effect of different abiotic gradients and their interconnectability on the explaining of species zonation in a specific mangrove site. We focus on the zonation patterns documented in Piou et al. (2006, Chapter 3) for Calabash Cay, Belize. The species zonation pattern was of particular interest for this site since it was the result of regeneration on the last 41yr after Hattie, a catastrophic hurricane that destroyed most of the mangroves in October 1961. The fact that McKee (1995a) demonstrated that crab predation does not play any role in Belizean species zonation pattern allowed us to discard a priori this aspect, which would ask for much more complex models to be tested. Thus, considering the Calabash sites we could test if differential dispersal of propagules, an influence of a nutrient or salinity gradient on individual growth, or

a combination of the effects of these abiotic gradients could reproduce well the creation of the mangrove zonation patterns after Hattie.

5.3 Methods

5.3.1 The KiWi model

We used the spatially explicit mangrove model KiWi (Berger and Hildenbrandt 2000), to simulate 41yr of regeneration of the four sites (A to D) described by Piou et al. (2006, Chapter 3) around Calabash Cay, Belize (See map of sites in figure 3.1). The growth function used in KiWi (Chen and Twilley 1998, Berger and Hildenbrandt 2000) was already parameterized for the three main Caribbean species: *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*. Site A had 4 zones parallel to the shore successively when going from the shoreline to the hinterland, and a length of 100m perpendicular to the shore. Site B had 4 zones and a length of 190m. The first 3 zones (out of 6) of site C described in Piou et al. (2006, Chapter 3) were dwarf areas with trees <3m. Thus, trees did not have a proper diameter at breast height, which is essential for the growth function used in KiWi. Therefore, we simulated for the present only the last 3 zones of site C, which had then a length of 60m. The site D had 3 zones and a length of 35m. The patterns to be reproduced were the values of basal areas (*BA*) of each of the 3 species in each zone. Thus, in total 12 *BA* were to be reproduced in sites A and B, while 9 *BA* in sites C and D. The simulation areas had the respective length for each site and always a width of 50m.

The individual trees in the KiWi model were managed with four main processes: recruitment, growth, mortality and spatial competition. The FON was the basis of many decision on the three other processes (see below). Thus, we start by explaining the competition processes and follow with the remaining processes.

Competition for spatial resource

We described inter-individual spatial competition using the FON approach (Berger and Hildenbrandt 2000), simulating the area where a tree influenced its neighbors and was influenced by them in their resource use. We assumed all spatially distributed resources (light, nutrients, ground water, etc . . .) to be phenomenologically integrated in this approach. We assumed an exponential decrease of resource use going away from the stem (trunk) position by applying an intensity field on top of the influenced area. Thus, the FON

specified the strength of competition exerted by a tree at any position within its neighborhood:

$$FON(r) = \left\{ \begin{array}{ll} 1 & \text{for } 0 \leq r < rbh \\ \exp\left(-\frac{|\log(F_{min})|}{R-rbh} \times (r-rbh)\right) & \text{for } rbh \leq r \leq R \\ 0 & \text{for } r > R \end{array} \right\} \quad (5.1)$$

where rbh was the radius of the stem at breast height and F_{min} was the minimum intensity (0.1) of the FON at the FON radius (R). The FON radius R of a tree depended on its size:

$$R = a \times rbh^b \quad (5.2)$$

where a and b were scaling parameters. The parameterization of a and b was possible to effectuate with the relationship among mean tree diameter at breast height (dbh) and tree density during a self-thinning phase (cf Appendix A of Chapter 4, page 107, for the description of these fits and the explanation of the selected values). We used for this study the species-specific a and b values coming from data of Belizean monospecific mangrove stands (Chapter 4). This setting assured that if a species would colonize an empty area without the other two species, the patterns of exponential relationship among dbh and density, occurring normally in self-thinning situation, and documented from monospecific stands of Belize, would be reproduced (cf Appendix A of Chapter 4, page 107).

Recruitment

a) Number of invading saplings

Recruits were established on the simulation area at the beginning of the simulation and at each time step. These recruits were considered as already grown up individuals of $dbh = 2\text{cm}$. The number of invader N_{inv} at starting conditions was tested as a varying parameter because the range of number of initial recruits (i.e. the ones assumed to recolonize the area on the first year of recovery) were not known precisely. We tested 4 values: 100, 500, 1000 and 5000 saplings/ha. The three species had equal proportions of saplings within these first recruits.

The number of new recruits per time step was calculated for each species as the sum of the potentially produced recruits of each tree (N_s). This relationship was adapted from empirical regression between tree size and fruits and flower production for *Rhizophora spp* and non-*Rhizophora spp*

(Komiya 1988 in Saenger 2002). We transformed the exponential structure of the original regression formula to a polynomial structure for facilitating computing. We assumed a necessary weight of 30g of flower/fruits production to obtain one potentially surviving *R. mangle* seedling and of 10g to obtain one potentially surviving seedling of *A. germinans* and *L. racemosa* (Fig. 5.2). Thus the production of each tree was calculated as:

$$N_s = \alpha \times dbh^3 + \beta \times dbh^2 + \delta \times dbh + \epsilon \quad (5.3)$$

where α , β , δ and ϵ were species-specific parameters (Table 5.1). The parameterization was identical for *A. germinans* and *L. racemosa* and assumed that trees of these species produced higher number of recruits than *R. mangle* trees for identical size.

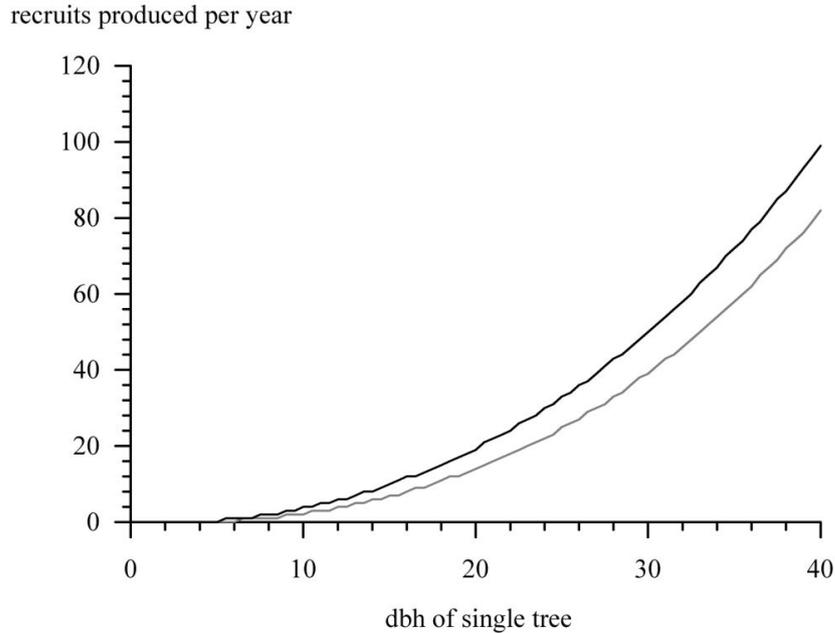


Figure 5.2: Annual production of potential recruits of a single tree according to its diameter at breast height (*dbh*) (black line: *Avicennia germinans* and *Laguncularia racemosa*, grey line: *Rhizophora mangle*) according to equation 5.3 and parameters used in table 5.1.

b) Influence of tidal sorting

The tidal sorting of propagules has been often proposed as an explanation of species zonation pattern (e.g. Rabinovitz 1978, Jiménez and Sauter 1991). We tested three cases of influence of tides on the establishment of new recruits. The first case, as a null hypothesis, was considering no influence of tides on the establishment of recruits (referred to as *TideO*). The invading saplings were therefore randomly distributed. The second case (referred to as

TideThresh) assumed that the saplings of the different species could settle anywhere until a species-specific maximum tidal range. It assumed that the influence of the tide and wave action would exclude some species of the lower intertidal only (Fig. 5.3a). To simulate that, we calculated a probability to settle (P_s) at a specific point depending on the maximum tidal level at this point (MTL , in cm) and the species of a considered sapling with the following formula:

$$P_s = \frac{1}{1 + \exp -0.5 \times (td_1 - MTL)} \quad (5.4)$$

where td_1 was a species-specific constant (table 5.1, estimated from the highest maximum tidal level where the species was found in Calabash Cay minus 5cm). The third case assumed also an effect of the maximum tidal level but on both sides of the species distribution (referred to as *TidePar*). This simulated an effect of wave and tide action on the lower intertidal but also that species with big seedlings (such as *R. mangle*) would less likely arrive to high grounds (Fig. 5.3b). We calculated the probability to settle with the following formula:

$$P_s = \frac{-0.5 + td_2 \times MTL - 0.5 \times MTL^2}{td_3} \quad (5.5)$$

where td_2 and td_3 were species specific constants (table 5.1, td_2 was estimated from half of the highest maximum tidal level where the species was found in Calabash Cay, td_3 was standardized so that the probability go up to 1.0). In both of these latter cases (*TideThresh* and *TidePar*), new individuals were proposed to establish at randomly chosen points. Each individual had already an assigned species according to the proportions described above (page 119). The probability to settle at this point was calculated with species-specific parameters (on Eq. 5.4 or 5.5) and tested against a uniform random number between 0 and 1. If the random number was higher than the P_s , the recruit was sent randomly somewhere else until finding a suitable place. Doing so, the proportion of recruits from different species was not reduced by the proportion of suitable habitat. The maximum tidal level (MTL) for each point of a site was available in the model from site-specific bitmaps representing the gradient of MTL measured by Piou et al. (2006, Chapter 3) in the 4 sites of Calabash Cay. The first invaders were established at the beginning of the simulations according to the version of these tidal effects, while the yearly new ones were settled also depending on the strength of the competition at the point where the tidal sorting lead them (see below).

c) Influence of competition intensity of already established trees on recruitment

After the influence of tidal sorting on the ending position of a recruit, the model tested if the sapling could actually have grown up at this place. We calculated for each new yearly recruit the sum of the FON intensity F of the already established trees at its stem position $(x_{recruit}, y_{recruit})$:

$$F(x_{recruit}, y_{recruit}) = \sum_{i=1}^n FON(Dist_i) \quad (5.6)$$

where n was the number of neighboring trees influencing at $(x_{recruit}, y_{recruit})$ and $Dist_i$ was the distance of $(x_{recruit}, y_{recruit})$ to the neighbor stem position. The sum F was then compared to a species-specific threshold value (Max_F , table 5.1). This handling prevented recruits from becoming a tree of $dbh=2\text{cm}$ if the F value was above Max_F . Although the FON approach assume all spatial resources, these values of Max_F represented a capacity of the recruits to deal with shadow. These thresholds simulated the shade intolerance of seedlings of *L. racemosa* and *A. germinans* (Ball 1980, McKee 1993).

Growth

The growth of each individual tree was calculated with the following formula (Berger and Hildenbrandt, 2000):

$$\frac{ddbh}{dt} = \frac{G \times dbh \times \left(1 - \frac{dbh \times H}{dbh_{max} \times H_{max}}\right)}{274 + 3 \times b_2 \times dbh - 4 \times b_3 \times dbh^2} \times f_s(SALT) \times f_n(RNA) \times f_c(F_A)$$

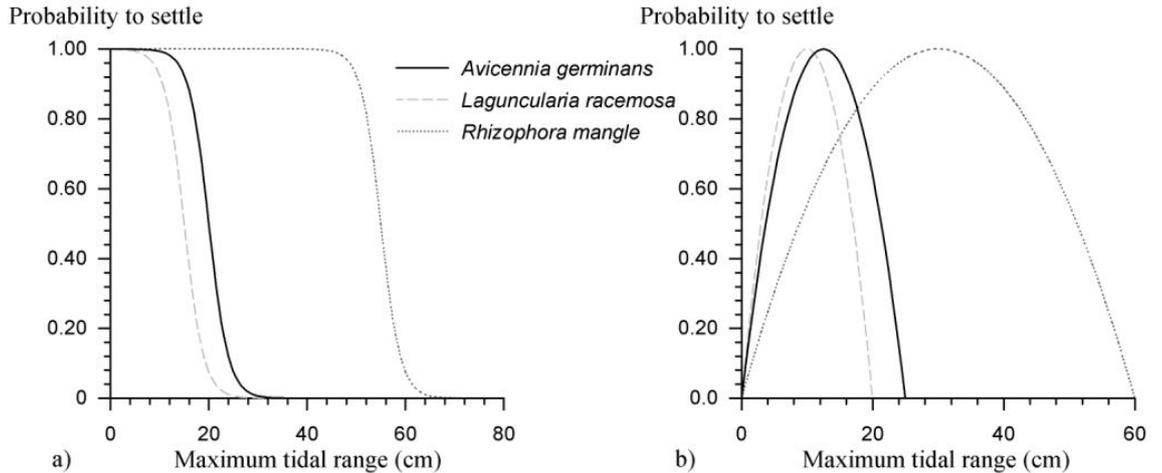


Figure 5.3: Sub-models of probability to settle depending on the species and the maximum tidal range. a) sub-model of threshold type of tide influence on settling (*TideThresh*). b) sub-model of parabolic type of tide influence on settling (*TidePar*).

(5.7)

where dbh was the stem diameter at breast height (cm); H was the tree height (cm); dbh_{max} and H_{max} were maximum values of diameter and height for a given tree species (Table 5.1); G , b_2 and b_3 were species-specific growth constants (Table 5.1). The multipliers $f_s(SALT)$, $f_n(RNA)$ and $f_c(FA)$ were respectively simulating the negative effect of pore water salinity, relative nutrient availability and spatial competition on growth. They returned values between 0 and 1 depending respectively on the local salinity, the local nutrient availability and sum of Field Of Neighborhood (FON). The parameterizations of these multipliers were also species-specific. The salinity multiplier was taken from Chen and Twilley (1998):

$$f_s(SALT) = \frac{1}{1 + \exp(d \times (S_{0.5} - S))} \quad (5.8)$$

where d and $S_{0.5}$ were species-specific parameters (Table 5.1) and S was the local salinity. The local salinity was given in KiWi by a bitmap map reproducing the maximum values measured per zone along the intertidal by Piou et al. (2006, Chapter 3). To test the effect of this salinity gradient on the species zonation another set of simulations were done with a homogeneous benign salinity across all the zones of all sites $S = 45\text{psu}$. The salinity gradient parameterization was referred to as *SalinityGrad* while the other was referred to as *HomogeneousSal*.

The relative nutrient availability multiplier was also computed after Chen and Twilley (1998):

$$f_n(RNA) = c_1 + c_2 \times RNA + c_3 \times RNA^2 \quad (5.9)$$

where c_1 , c_2 and c_3 were species-specific parameters (Table 5.1) and RNA was the local relative nutrient availability also given by an underlying bitmap. The relative nutrient availability was indicated by Chen and Twilley (1998) as an indicator of relative phosphorous availability, which they believed to be the most limiting nutrient in their sites. In our focus sites, phosphorous and nitrogen might be limiting factors of growth (Piou et al. 2006, Chapter 3). However, if they had any limiting effects it had to be stronger on the shorelines than inside since Piou et al. (2006, Chapter 3) observed decrease of nutrient use efficiency from the shore to the hinterland, indicating an inverse availability pattern. We tested consequently two settings of nutrient availability to analyze if a gradient had an effect on the species zonation: a homogeneous $RNA = 60\%$ (hereafter referred to as *HomogeneousNut*) and a gradient of RNA from 50% on the shore to 70% inland (hereafter referred

to as *NutrientGrad*). The homogeneous value was selected to represent the overall nutrients limitation that occur on offshore mangrove islands on oligotrophic waters such as on the Calabash Cay. The gradients values were selected to still allow all species to grow on all areas ($RNA > 40\%$, see Chapter 4, see Fig. 4.1), and simulating approximately a range of variation of nutrient availability that the resorption efficiency and nutrient use efficiency measured on those sites indicated (Chapter 3, see Fig. 3.3 and 3.4).

The competition multiplier reducing the growth rate of a single tree was computed as proposed by Berger and Hildenbrandt (2000) as depending on the sum of all neighbors FON effect:

$$f_c(F_A) = \max \left\{ 0 \ ; \ 1 - 2 \times \left(\frac{1}{A} \sum_{n \neq k} \int_O FON_n(x, y) dO \right) \right\} \quad (5.10)$$

where n are the neighbors of the focus tree k , A was the FON area of k and O was the overlap area between the FON area of k and each n . As mentioned earlier the species-specific parameterization of the FON radius calculation (R , Eq. 5.2) gave different spatial competition strength to the three species. For two theoretical individuals of identical dbh and close enough to have overlap of their FON areas, the one having the smaller R felt the most the competition effect (Berger et al. 2002). Thus in our setting of R calculation, the competition strength for most sizes of dbh of our focus 41yrs was following the order described by Ball (1980): *R. mangle* > *A. germinans* > *L. racemosa*.

Mortality

The KiWi model simulated mortality as a consequence of growth repression during a certain time period. The mean dbh increase over the last 5 yrs was computed per individual and compared to a species-specific threshold ($Crit\Delta dbh$, table 5.1). If this mean dbh increase was below the $Crit\Delta dbh$ the tree was set to die and removed from the simulation area. This method of mortality coupled with the FON approach has been seen to reproduce several patterns of biomass-density trajectories and size distributions of living dead trees (Berger et al. 2002) and allow a more mechanistic mortality process than with random removal.

5.3.2 Simulations and analysis

We simulated 20 times each sites with all the possible combination of the sub-models (Table 5.2, leading to 48 possible parameterizations). For each

Table 5.1: Species-specific parameters used in the KiWi model. Sources: (1) Chen and Twilley 1998, (2) Chapter 4, (3) Estimations from Piou et al. 2006 (Chapter 3) data, (4) Estimations.

Parameter	Description (Equation and units if applicable)	<i>A. germinans</i>	<i>L. racemosa</i>	<i>R. mangle</i>	
a	FON radius scaling parameter (Eq. 5.2)	13.7	17.0	18.0	(2)
b	FON radius scaling parameter (Eq. 5.2)	0.72	0.95	0.83	(2)
α	Constant for dbh to sapling relationship (Eq. 5.3)	0.0004	0.0004	0.0006	(3)
β	Constant for dbh to sapling relationship (Eq. 5.3)	0.0489	0.0489	0.0302	(3)
δ	Constant for dbh to sapling relationship (Eq. 5.3)	-0.2026	0.2026	-0.1641	(3)
ϵ	Constant for dbh to sapling relationship (Eq. 5.3)	0.0	0.0	0.2401	(3)
td_1	Constant in tidal effect function of TideThresh sub-model (Eq. 5.4)	20.00	15.00	55.00	(3)
td_2	Constant in tidal effect function of TideParab sub-model (Eq. 5.5)	12.50	10.00	30.00	(3)
td_3	Constant in tidal effect function of TideParab sub-model (Eq. 5.5)	0.0077625	0.00495	0.04495	(3)
Max_F	Maximum FON intensity for establishment	0.0	0.0	0.5	(4)
dbh_{max}	Maximum diameter at breast height (Eq. 5.7, cm)	140	80	100	(1)
H_{max}	Maximum height (Eq. 5.7, cm)	3500	3000	4000	(1)
G	Growth constant (Eq. 5.7)	162	243	267	(1)
b_2	Constant in height to dbh relationship (Eq. 5.7)	48.04	71.58	77.26	(1)
b_3	Constant in height to dbh relationship (Eq. 5.7)	0.172	0.447	0.396	(1)
d	Salinity effect constant (Eq. 5.8)	-0.18	-0.20	-0.25	(1)
$S_{0.5}$	Salinity effect constant (Eq. 5.8, psu)	72.0	65.0	58.0	(1)
c_1	RNA effect constant (Eq. 5.9)	-0.50	-1.00	0.00	(1)
c_2	RNA effect constant (Eq. 5.9)	2.88	4.42	1.33	(1)
c_3	RNA effect constant (Eq. 5.9)	-1.66	-2.50	-0.72	(1)
$Crit\Delta dbh$	Mean dbh increase threshold (cm.yr ⁻¹)	0.23	0.20	0.20	(4)

parameterization replicate we recorded the final position, dbh , and species of all the trees present at the end of the simulations (41yrs). We then applied the same sampling technique as in Piou et al. (2006, Chapter 3) to be able to compare real data with simulation data of identical precisions. This sampling was using a point center quarter method (PCQM) (Cintr3n and Schaeffer-Novelli 1984) with 21 random points across each zone from which

Table 5.2: Sub-models (with corresponding hypothesis of effect on species zonation pattern) and parameter varied in our analysis to arrive to the 48 possible cases.

Simulated aspects	Cases	Sub-models or variables	Tested hypothesis influencing species zonation
First recruitment	4	Density of invaders: 100, 500, 1000 and 5000 saplings/ha	
Tidal sorting	3	<i>TideO/TideThresh/TidePar</i>	Tidal sorting of recruits depending on elevation along the intertidal
Salinity	2	<i>HomogeneousSal/SalinityGrad</i>	Species adaptations to gradients of salinity
Nutrient availability	2	<i>HomogeneousNut/NutrientGrad</i>	Species adaptations to gradients of nutrient availability

the distance of the 4 closest trees in respective 4 quadrats around the point were noted as well as their species and *dbh*. Out of these measurements, the basal area (*BA*) per species per zone was evaluated. We repeated the random PCQM sampling 10 times per replicate simulation results. This led us to 200 observations of *BA* of the 3 species per zones of each sites to be compared to the field data. The patterns of focus to be reproduced were therefore each field value of basal area (*BA*) per species per zone (not shown in Piou et al. 2006, Chapter 3, but presented in figure 5.4).

We then applied the pattern-oriented modeling information criterion (*POMIC*) approach presented in Chapter 2 to estimate the likelihood of a simulation parameterization to reproduce each *BA* values of the 3 species in all the zones of a given site. For each species in each zone the 200 *BA* simulation results (vector *BA*s) were first transformed with a Gaussian kernel density estimator (R Development Core Team 2006) of band width (*bw*) calculated as:

$$bw \cong \frac{\max(BAs) - \min(BAs)}{10} \quad (5.11)$$

where $\max(BAs)$ and $\min(BAs)$ were the maximum and minimum of *BA*s respectively. The resulting densities (vector *D*s) were then scaled into probabilities of observation of *BA* values (*P*s):

$$Ps = \frac{Ds}{\max(H)} \quad (5.12)$$

where $max(H)$ was the maximum probability value obtained in a histogram of probability drawn with BAs and class widths bw . These Ps values were always 512 values (standard of the R Gaussian kernel density estimator) corresponding to a vector BA_P of 512 BA values of range $BA_{P_{range}} = [\text{minimum } BA \text{ returning a } D_s > 0 (BA_{min_D}), \text{ maximum } BA \text{ returning a } D_s > 0 (BA_{max_D})]$ and of constant increment ($BA_{P_{step}}$):

$$BA_{P_{step}} = \frac{BA_{max_D} - BA_{min_D}}{511} \quad (5.13)$$

To estimate the likelihood of a simulation result to have reproduced a field observation $L(BA_{field}|parameterization)$ we then used the Ps value of the corresponding BA_P value the closest to the field BA (BA_{field}):

$$L(BA_{field}|parameterization) = \left\{ \begin{array}{ll} Ps[k] & \text{if } BA_{field} \in BA_{P_{range}} \\ 0 & \text{otherwise} \end{array} \right\} \quad (5.14)$$

where k was the position in BA_P where $BA_P[k]$ was the closest to BA_{field} . We then applied the following formula to calculate the $POMIC_s$ of a site s for each parameterization (Chapter 2):

$$POMIC_s = \frac{1}{3 \times Z} \sum_{zone=1}^Z \sum_{sp=1}^3 \log(L(BA_{field}|parameterization)) \quad (5.15)$$

where Z was the number of zones in the respective site s and sp was corresponding to one of the three species. This criterion was developed as a goodness of fit indicator for pattern-oriented studies done with individual-based models. The smaller the value of $POMIC$, the better the pattern was reproduced. If the $L(BA_{field}|parameterization)$ of only one species in one zone was 0, the $POMIC$ would become infinite. This would mean a lack of representation of the parameterization to reproduce the focus basal area of a species in one zone of this site. To be able to compare parameterizations even in the case that all of them led to one species not reproduced in one zone, we used an adaptation of the $L(BA_{field}|parameterization)$ and counted how many times the BAfield was not element of $BA_{P_{range}}$ (find in the ‘‘Number of unmatched patterns’’ variable presented in the results):

$$L(BA_{field}|parameterization) = \left\{ \begin{array}{ll} Ps[k] & \text{if } BA_{field} \in BA_{P_{range}} \\ 10^{-323} & \text{otherwise} \end{array} \right\} \quad (5.16)$$

This allowed us to still observe what the best parameterizations were for all the other species and zones of this site.

Single values of *POMIC* do not inform much, so for each site we computed the *POMIC* differences for each parameterization i :

$$\Delta_{s,i} = POMIC_{s,i} - POMIC_{s,min} \quad (5.17)$$

where the $POMIC_{s,min}$ was the minimum $POMIC_s$ value among all parameterizations. These differences were used to compute the probability of a parameterization to be the best one among the set of parameterizations Λ tested to represent a given site s (Chapter 2):

$$W_{s,i} = \frac{\exp(-\Delta_{s,i})}{\sum_{\lambda=1}^{\Lambda} \exp(-\Delta_{s,\lambda})} \quad (5.18)$$

These weights of evidence in favor of each parameterization i were the basis of our discussions about the processes that might have happened in each site of Calabash Cay between 1961 and 2002. All analyses were effectuated with scripts developed for the R software ©(version 2.3, 2006).

5.4 Results

No parameterization tested reproduced all the basal area patterns of site A (Table 5.3). These unmatched patterns were due to a too high presence of *A. germinans* on all but the first zone of the site (Fig 5.4a). The best fitting parameterization and the second best had only one unmatched pattern, but the weight of evidence showed that the best parameterization was much more likely (70%) to be correct than the second (30%) or any other ones (Table 5.3). From these two best parameterizations, the results showed that to reproduce the best the species basal area, the model needed to include a tidal sorting process according to the supposed resistance of propagules to wave action (*TideThresh*).

The parameterizations tested did not reproduce entirely the basal area patterns of site B (Table 5.4). A set of 9 parameterizations were found with only one pattern of basal area not reproduced: the basal area of *L. racemosa* in the first zone, which was always 0.0m²/0.1ha in our simulations but close to 2.0m²/0.1ha in the field (Fig 5.4b). This set of 9 parameterizations included the salinity gradient influence (*SalinityGrad*, Table 5.4). The weights of evidence were shared among these 9 parameterizations with 6 of them with $W_i \geq 0.1$. These 6 best parameterizations showed that to obtain a good fit, the nutrient gradient was not necessary. They also showed that it was better to use the tidal effect parameterization *TidePar*, and that the number of initial recruits did not matter.

Table 5.3: Best 12 parameterizations of simulations of site A leading to the reproduction of the species-specific basal area patterns. (*Rec* = First recruitment /ha, *Num* = Number of unmatched patterns)

<i>Rec</i>	Tidal sorting	Nutrient availability	Salinity	<i>Num</i>	<i>POMIC_i</i>	Δ_i	W_i
100	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>HomogeneousSal</i>	1	63.56	0	0.7
100	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	64.43	0.87	0.3
100	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	2	122.25	58.69	0
100	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>HomogeneousSal</i>	2	122.43	58.87	0
1000	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	3	181.92	118.36	0
1000	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>HomogeneousSal</i>	3	181.93	118.37	0
5000	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	3	181.99	118.43	0
100	<i>TidePar</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	3	182.03	118.47	0
100	<i>TidePar</i>	<i>NutrientGrad</i>	<i>HomogeneousSal</i>	3	182.05	118.49	0
500	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	3	182.09	118.53	0
500	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>HomogeneousSal</i>	3	182.1	118.54	0
1000	<i>TidePar</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	3	182.11	118.55	0
Any other parameterization combination				≥ 3	> 182.11		0

Table 5.4: Best 12 parameterizations of simulations of site B leading to the reproduction of the species-specific basal area patterns. (*Rec* = First recruitment /ha, *Num* = Number of unmatched patterns)

<i>Rec</i>	Tidal sorting	Nutrient availability	Salinity	<i>Num</i>	<i>POMIC_i</i>	Δ_i	W_i
500	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	61.89	0	0.18
1000	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	62.11	0.23	0.14
100	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	62.16	0.27	0.14
5000	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	62.27	0.38	0.12
500	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	62.36	0.48	0.11
100	<i>TideO</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	62.48	0.6	0.1
1000	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	62.56	0.67	0.09
1000	<i>TideO</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	62.97	1.09	0.06
1000	<i>TidePar</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	1	63.11	1.23	0.05
5000	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	2	121.93	60.05	0
100	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	2	122.02	60.13	0
100	<i>TidePar</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	2	122.13	60.25	0
Any other parameterization combination				≥ 2	> 122.13		0

Simulations of site C obtained 11 cases of parameterizations fitting well enough to match the patterns (Table 5.5). These cases shared very close weights of evidence, meaning that none really outstood the others. Most (9 out of 11) of these cases used the sub-model of gradient of salinity (*SalinityGrad*) indicating an importance of this effect. The other aspects (tidal sorting effect, nutrient gradient or number of initial recruits per hectare) did not appear to be important on their own to have a good fit. The best fitting simulation

Table 5.5: Best 12 parameterizations of simulations of site C leading to the reproduction of the species-specific basal area patterns. (*Rec* = First recruitment /ha, *Num* = Number of unmatched patterns)

<i>Rec</i>	Tidal sorting	Nutrient availability	Salinity	<i>Num</i>	<i>POMIC_i</i>	Δ_i	W_i
1000	<i>TideO</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	0	2.71	0	0.12
1000	<i>TideO</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	2.72	0.01	0.12
100	<i>TideO</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	2.75	0.05	0.12
5000	<i>TideO</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	0	2.86	0.15	0.11
100	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	2.94	0.23	0.1
500	<i>TideO</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	2.96	0.25	0.1
100	<i>TideO</i>	<i>NutrientGrad</i>	<i>HomogeneousSal</i>	0	3.03	0.33	0.09
5000	<i>TideO</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	3.14	0.43	0.08
500	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	3.25	0.55	0.07
5000	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	3.3	0.59	0.07
500	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>HomogeneousSal</i>	0	3.92	1.21	0.04
100	<i>TideO</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	1	82.34	79.64	0
Any other parameterization combination				≥ 1	> 82.34		0

had always an over-estimation of *BA* of *L. racemosa* in the third zone, and the presence of *R. mangle* in the second zone was also not well reproduced (Fig 5.4c).

The site D obtained 6 parameterizations matching all the basal area patterns (Table 5.6). For a good fit, a salinity gradient effect and/or a nutrient gradient effect were necessary. The tidal sorting effect was not important on its own. Figure 5.4d shows that the patterns of species dominance in *BA* among zones were well reproduced by the best parameterization of this site.

Finally, no plain null hypothesis parameterization (using only null sub-models: *TideO*, *HomogeneousNut* and *HomogeneousSal*) with any number of recruits per hectare entered within the first quarter of the best parameterization of each sites.

5.5 Discussion

This study analyzed some potential processes of influence of abiotic gradients at the origin of species zonation patterns of 4 mangrove sites of an offshore island. Our simulation results show that overall, the Calabash Cay zonation patterns could have their origins in abiotic conditions: a tidal gradient influencing recruit establishment and/or a salinity gradient influencing local species growth. This is concordant with what proposed Piou et al. (2006, Chapter 3) for this specific site, and with other mangrove ecology

Table 5.6: Best 12 parameterizations of simulations of site D leading to the reproduction of the species-specific basal area patterns. (*Rec* = First recruitment /ha, *Num* = Number of unmatched patterns)

<i>Rec</i>	Tidal sorting	Nutrient availability	Salinity	<i>Num</i>	<i>POMIC_i</i>	Δ_i	W_i
100	<i>TideThresh</i>	<i>NutrientGrad</i>	<i>HomogeneousSal</i>	0	2.83	0	0.24
100	<i>TideO</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	0	2.86	0.03	0.23
100	<i>TideO</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	3.06	0.23	0.19
1000	<i>TideThresh</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	0	3.19	0.35	0.17
500	<i>TideO</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	0	3.63	0.8	0.11
1000	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	0	3.99	1.15	0.07
100	<i>TidePar</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	82.47	79.64	0
500	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>HomogeneousSal</i>	1	82.78	79.95	0
100	<i>TideThresh</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	1	82.79	79.96	0
500	<i>TideThresh</i>	<i>NutrientGrad</i>	<i>SalinityGrad</i>	1	82.94	80.1	0
100	<i>TideThresh</i>	<i>HomogeneousNut</i>	<i>SalinityGrad</i>	1	82.95	80.11	0
100	<i>TideO</i>	<i>NutrientGrad</i>	<i>HomogeneousSal</i>	1	83.09	80.26	0
Any other parameterization combination				≥ 1	> 83.09		0

studies (e.g. McKee 1995b). Additionally, our study differentiated between the relative importances of the different processes entering into play for each specific site.

We observed that the site B, on the north-eastern side of the island, could have its patterns of basal areas apparently driven by the combined effect of a strong salinity gradient and the initial establishment of recruits following a tidal sorting. The selected tidal sorting process was a limitation on both sides of the range of dispersion of the species, assuming a combined action of wave action limiting the lowest range, and seed transport limiting the highest range. Identically, a tidal sorting process was likely to be the main process leading to zonation for the site A. However, for this site the selected tidal sorting process was a limitation on the lower range of establishment only, assumed to be because of wave action. These 2 sites were on the North-eastern (seaward) side of Calabash Cay. On the other side, the sites C and D did not need tidal sorting to reproduce their patterns of basal areas. They appeared to be under the effect of a gradient of salinity or nutrient availability on individual growth. This might be related to the western position of these sites C and D, where they are more protected against high tides driven by the wind and therefore maybe less influenced by tidal regimes. Additionally, Piou et al. (2006, Chapter 3) argue that the protected situation of these 2 sites allow more survival on this side of the island. This was proposed as influencing the homogeneity of species dominance within the zones in Piou et al. (2006, Chapter 3), and as producing a quite high availability of seedling on this side of the island. The *L. racemosa* and *A. germinans* seeds

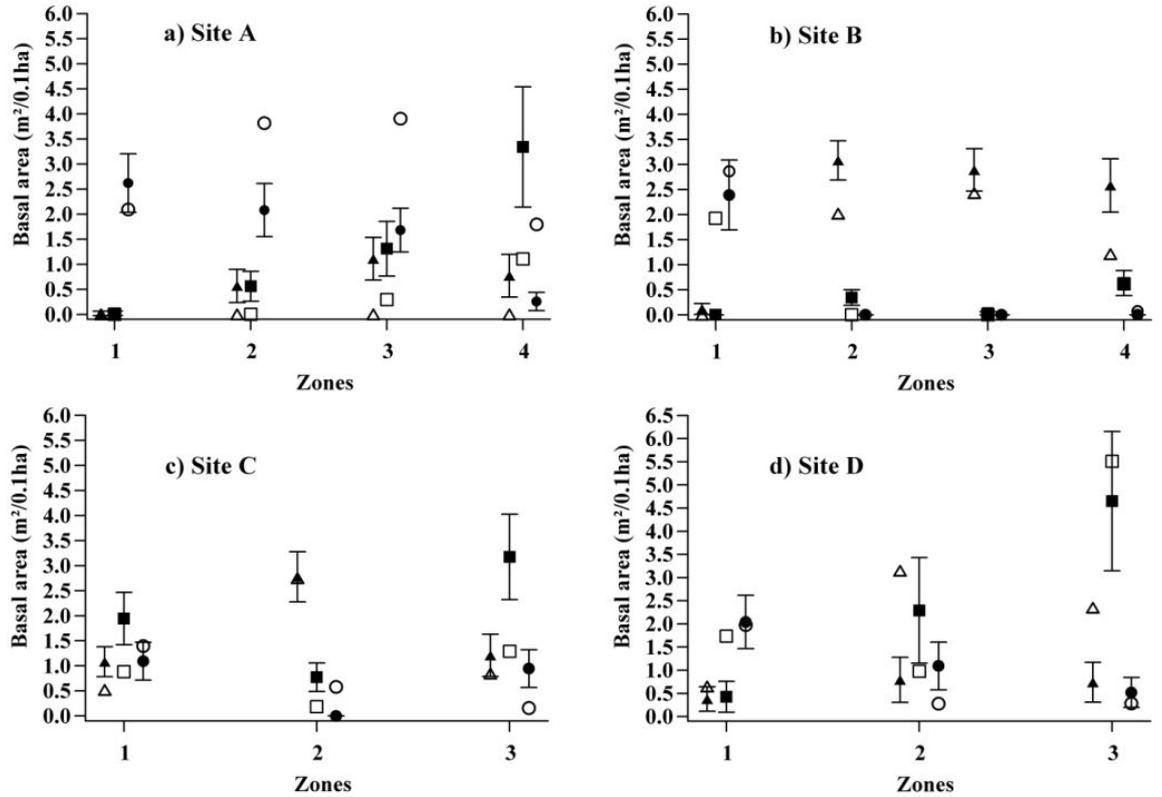


Figure 5.4: Field observed basal areas (open marks) and best KiWi simulation results (filled marks) per species (triangles=*A. germinans*, squares=*L. racemosa* and circles=*R. mangle*) and zones of the four sites (a to d) of Calabash Cay. Error bars of simulation results represent the standard deviation of 200 values. The best simulations were selected as the parameterizations obtaining the smallest *POMIC* value per sites (the first line of the tables 5.3 to 5.6 respectively).

could probably come from the big trees that survived Hattie the most inland, while the *R. mangle* ones could have been produced by the dwarf trees that survived the hurricane (Piou et al. 2006 Chapter 3).

The lack of reproduction of some basal area patterns of site A might be also linked to seed availability question. Piou et al. (2006, Chapter 3) proposed that succession might have lead to these homogeneous zones on the eastern side of Calabash Cay. On the present simulation study, we did reproduce species dominance succession with the species-specific parameters as in Chapter 4. Thus, there was probably another process to explain why no *A. germinans* were found on the site A on the field. The simulations showed that this species could grow there, with or without an effect of the abiotic gradients. We should test with other simulations if changing the initial species

ratio of seed availability would reproduce the patterns of basal area for site A. However, another process not simulated on our study might be that the site A topography could have changed during the last 41 yrs. The fact that *R. mangle* trees in the 3 first zones of this site is often found in bunch of stems spreading in all directions from a center point (C. Piou and I.C Feller, personal observations) could be a tree architecture characteristic that indicates an initial establishment of sparse *R. mangle* trees forming small “islands” of colonization and sediment-trap. Actually, this type of island structure is now found on the fringe zone of site A. By sedimentation and peat production around these islands originally over-washed, the first 3 zones of site A might have increased in elevation compared to 1961. Thus, previous lower elevation could have retained *A. germinans* seedling to establish. Obviously, before arguing further in favor of this often refuted land-building hypothesis (Davis 1940, or see Bertrand 1999), one should also test other hypothesis of processes that lead to the absence of *A. germinans* on this site.

The non-reproduction of the presence of *L. racemosa* on the first zone of site B is another problematic pattern. The tidal effect obviously does not let this species establish on this zone in KiWi (e.g. best first 5 simulations). And with no tidal effect simulated (for 6th best parameterization in table 5.4), the model leads to the presence of *A. germinans* on this first zone while it was not seen on the field data. Assuming that tidal sorting effect would have occurred on site B, a process in change of elevation could be a reason of presence of *L. racemosa* in the first zone. These *L. racemosa* were observed with cable roots that should normally be buried, on the surface of the sediment. Thus, a sand bank might have been left there after Hattie, where individuals from this species could establish, and an erosion process from waves of minor storms could have then removed this sediment. Thus, historic configuration probably played an important role in site A and B recovery and their species zonation patterns. Eventually, palynological works on palaeo-vegetation (e.g. Behling et al. 2001) and analysis of sediment origin (e.g. Marchand et al. 2003) could enhance the historic knowledge on these 2 specific sites to answer the questions of presence/absence of species.

We assumed in our study that interspecific competition occur at the level of the individual trees among the three Caribbean mangrove species. We considered for that different growth capacities with species-specific parameters, as well as species-specific capacities of spatial competition for resource simulated with the FON approach. The objective was to test the effects of abiotic gradients and tidal sorting assuming an underlying competition. Nevertheless, with the simulations using no effect of tidal sorting and abiotic gradients, we indirectly tested if competition among individuals could appear to be a process explaining alone the zonation patterns. We observed that it did not.

We did not test directly if the abiotic gradients and tidal sorting assuming no underlying competition (no species-specific differences in growth parameters, or in FON parameters) could lead to the reproduction of the basal area patterns. However, using other FON settings or growth parameters would imply not to respect other patterns. We used a species-specific FON settings that assured that if a species would colonize an empty area without the other two, the patterns of relationship among *dbh* and density observed in monospecific stands of Belize would be reproduced (as in Chapter 4 - Appendix A, and first analyzed by Berger and Hildenbrandt 2003). Additionally, the species-specific growth parameters also reproduce patterns of relationship among *dbh* and height implemented in the first mangrove dynamic individual-based model (Chen and Twilley 1998). So under a pattern-oriented framework, the “no-interspecific-competition” scenario would anyway miss to reproduce these 2 important patterns. A recommendation for future work could be to assess the effect of lack of habitat partitioning proposed by Clarke (2004): testing if the establishment of saplings by proximity and with different capacity of coping with shade would, by itself, arrive to reproduce zonation patterns, or if it needs to be combined with other processes.

Finally, this study illustrated the importance of abiotic conditions on the creation of species zonation patterns in mangroves. Other pattern-oriented simulation studies such as the present one could assess further the different hypotheses illustrated in Figure 5.1. Evidence criteria based on information theoretic approach such as the *POMIC*, could help in ranking the importance of each process behind these hypotheses. Simulation studies would then lead to a clearer picture of the specific importance of each driving force. The scales of action of these forces could also be assessed and if they are to be considered as driving- or maintaining-forces for the mangrove species zonation patterns.

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Part II

Intraspecific competition in North Brazilian *Ucides* *cordatus* populations

Chapter 6

Spatial structure of a leaf-removing crab population in a mangrove of North-Brazil



Spatial structure of a leaf-removing crab population in a mangrove of North-Brazil

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6.1 Abstract

The ecological engineer and leaf-removing decapod crab, *Ucides cordatus* plays a key role in Brazilian mangrove ecosystems. We analyzed the spatial distribution of a specific population at different scales to observe how individual behavior could alter spatial distribution at population level. First, we conducted a spatial point pattern analysis of the burrow entrances and the *Rhizophora mangle* prop roots on the mangrove floor at scale of few meters. The burrow entrances, although aggregated around the prop roots, showed a regularly spaced distribution ($\sim 25\text{cm}$) signaling a probable effect of intraspecific competition among the crabs. Secondly, we analyzed at large scale ($>10\text{m}$) the effects of surface elevation, light intensity, prop root coverage, type of neighboring tree species (*R. mangle*, *Laguncularia racemosa*, *Avicennia germinans*) and pneumatophores density on the size and number of burrow entrances. This demonstrated the preference of the crabs to install their burrows at intermediate surface elevation and prop root coverage, and in *R. mangle*-dominated areas. Finally, still at large scale, we conducted an analysis of clustering of the crabs around the *R. mangle* trees. This confirmed the preference of aggregation around *R. mangle* trees in *R. mangle*-dominated forest, but not in *L. racemosa*-dominated forest. Food competition leading to the small scale regular patterns was hypothesized as an explanation for exclusion of smaller crabs from preferred habitats seen at large scale. This habitat preference and the observed transfer of influence of the feeding behavior from small to large scale might explain the variation of *U. cordatus* importance in Neotropical mangroves.

Key Words: *Ucides cordatus*, population structure, multiple scales, spatial statistics, habitat preference, intraspecific competition.

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6.2 Introduction

Burrowing organisms are ecosystem engineers par excellence (Jones et al. 1997). In mangrove ecosystems, burrowing decapod crabs may be the second most important group of physical ecosystem engineers after the tree themselves. Specifically, burrowing crabs are allogenic engineers (Jones et al. 1997) since they modify the habitats for other mangrove-floor inhabitants and for the trees (e.g., Warren & Underwood 1986, Smith et al. 1991). In the mangrove forests of northern Brazil, the burrowing crab *Ucides cordatus cordatus* L. 1763 (Ocypodidae) plays a key role in leaf removal, nutrient cycling processes (Schories et al. 2003, Nordhaus et al. 2006), and the trophic structure of these ecosystems (Wolff et al. 2000, Koch & Wolff 2002). *Ucides cordatus* is also economically important for this region where they are harvested intensively for human consumption (e.g., Glaser & Diele 2004, Diele et al. 2005). Thus, besides being ecosystem engineers, *U. cordatus* populations play a critical role in these highly productive macrotidal mangrove forests.

The distribution of *U. cordatus* is the tropical and sub-tropical mangrove coasts of the eastern Americas from southern Florida to southern Brazil (Bright & Hogue 1972). A closely related subspecies, *U. cordatus occidentalis* (sometimes refer to as *U. occidentalis*) is found on the Pacific side of the Americas from Baja California to northern Peru (Bright & Hogue 1972). In addition to Brazil, key ecological and/or economic roles for these crabs were reported only in the Guayas River Estuary in southern Ecuador (Twilley et al. 1997) and in the Dominican Republic (Geraldés & Calventi 1983). This scarcity of reports is not due to the lack of studies on Neotropical mangrove ecosystems, which have increased exponentially in the past 30 years. Many studies of Neotropical mangroves reported the presence of *U. cordatus* in other areas, e.g., Belize (Middleton & McKee 2001, McKeon & Feller 2004), Jamaica (Warner 1969), Costa Rica (Delgado et al. 2001), Panama (Sousa et al. 2003), Colombia (Cantera et al. 1999), French Guyana (Artigas et al. 2003). However, the biology of this crab has seldom been studied outside Brazil, probably due to either a lack of understanding of its importance in mangrove forests or the absence of large *U. cordatus* populations as in Brazilian forests. These observations lead Nordhaus et al. (2006) to ask what are the factors making *U. cordatus* populations more or less important for litter-processing role in different Neotropical mangroves. They demonstrated that the litter-processing role of sesarimid crabs in the Indo-Pacific mangroves is occupied by *U. cordatus* in northern Brazil (Nordhaus et al. 2006). These finding refuted the hypothesis that leaf litter processing is driven by herbivorous decapods in Indo-Pacific mangroves and by the detrital pathway in the

Neotropics (McIvor & Smith 1995).

To avoid these generalizations and understand the factors that drive these differences among mangrove ecosystems, we need to consider the problem of scale. It is unlikely that observations based on a small part of the distribution of *U. cordatus* hold for entire biogeographic biome. Levin (1992) argued that scale is central to interpreting ecological patterns and that to scale ecological processes from small to a higher level, one must understand how information is transferred. Levin also pointed out that patterns observed and understood at large scales are more often driven by external forces than at fine scales, which are generally autonomously generated. Thus, there are compounded risks to separate biogeographic patterns from findings derived locally. First, it would imply an external force significantly different in the two biogeographic biomes. Second, understanding local patterns does not assure that the same forces are driving larger scale patterns.

For burrowing and leaf-removing crabs, and particularly for *U. cordatus*, biological knowledge is rudimentary. One of the main challenges for ecologists is to understand the transfer of information from biological characteristics at the individual level to the population level or higher. This information transfer is understandable through the study of spatial patterns at different scale (e.g. Schooley & Wiens 2001, Rossi 2003a). Spatial patterns have been analyzed extensively for vegetation structure, landscape ecology, and soil ecology with statistical methods developed for >50 yr (e.g. Clark & Evans 1954, Diggle et al. 1976, Ripley 1977, Diggle & Gratton 1984, Rossi et al. 1992). Through characterizations of regular or clumped patterns of individuals at different scales and comparison with other type of events, one can understand which processes of interaction among individuals are stronger and how they influence the patterns at higher levels. A typical example is the regularity that appears during the growth of even-aged forest stands while individual trees compete for light and “self-thin” in clumped parts of the forest (e.g. Kenkel 1988). To our knowledge, the spatial distributions of burrowing decapods have not been analyzed. Investigations on the spatial patterns of ecosystem engineers are needed to increase our understanding of their influence on the distributions of other species (e.g. Schooley & Wiens 2001). But additionally, the understanding of the factors influencing spatial distribution of *U. cordatus* at different scales could lead to the identification of preferred habitat type that could later explain the absence of large *U. cordatus* population in some mangroves of the Neotropic and their local lack of importance in litter processing.

The present study examines first the spatial patterns of burrows of *U. cordatus* at small scale (<10m) in the mangrove ecosystems on the Caeté Peninsula, Brazil. The specific objective of this first approach was to investigate if

the interaction among crabs, which were seen as territorial and food limited (Nordhaus 2004, Nordhaus et al. 2006), led to competition-characteristic patterns of regular spatial distribution as plants do under competition for space. Second, we analyze the spatial distribution of these burrows in relation to *Rhizophora mangle* L. prop roots, which are assumed to provide crabs with refuge and burrow stability (Rademaker, unpublished manuscript). Third, we analyze the factors influencing the crab density and size at large scale (>10m), focusing on light availability, elevation of the ground, root zone occupation, and neighboring tree species which were the main factors hypothesized to influence *U. cordatus* population densities (Nordhaus et al. 2006). Finally, also at large scale, we study the clustering of crab burrows around *R. mangle* trees, whose leaves are the favorite food source for *U. cordatus* in this study area (Nordhaus 2004, Nordhaus et al. 2006).

6.3 Methods

6.3.1 Study area

The study areas were two mangrove sites of the Caeté Peninsula, the focus area of the long-term research project, Mangrove Dynamics and Management (MADAM, Berger et al. 1999). Mangroves covers 140 km² of this peninsula that is located just north of Bragança, 200 km east of Belém, Pará, Brazil (for more details see Wolff et al. 2000, Koch & Wolff 2002, Koch et al. 2005, Diele et al. 2005, Nordhaus et al. 2006). Our first site, called RF, was a *R. mangle*-dominated forest with sparse *Avicennia germinans* L. individuals on the north of the peninsula (within the site RF described by Nordhaus et al. 2006). The second site (~10km away), called LF, was dominated by *Laguncularia racemosa* (L.) Gaertn.f. with few *R. mangle* trees. This site was regenerating after the construction of a road across the peninsula during the 1970s (on the opposite side of the road of site AF described by Nordhaus et al. 2006). We selected these 2 sites to cover 2 types of vegetation found in the Caeté peninsula where *Ucides cordatus* is found in relatively high densities. Note that other types of vegetation are found in the peninsula, and local variations in dominance also occur, frequently linked to ground elevation.

6.3.2 Note on the sampling of burrows as proxy of crab population

Population estimations from burrow numbers have been used widely for other mangrove crab species (e.g. Macintosh 1988, Warren 1990, Skov et al. 2002, Salgado-Kent & McGuinness 2006). For the purposes of this study, we estimated that burrow counts and measurements were more practical than crab fishing. In the study area, crab collectors collect crabs by entering their bare arm into the burrows. This method leads always to the extensive disturbance of the muddy substrate. Other methods are used in other part of Brazil, but the local population is not aware of those and we preferred not to introduce them as it could entail the sustainability of the fishery (Diele et al. 2005). To test the assumption that burrow entrance was related to crab size, a preliminary survey was done during neap tides in the dry season of 2003 at site RF. Diameters of burrow entrances ($N = 310$) were measured to the nearest cm. The *U. cordatus* living on these burrows were fished, and their carapace widths were measured to the nearest mm. A non-parametric regression was applied to determine if there was a significant relationship between the entrance size and the carapace width of the crabs.

6.3.3 Spatial distribution of burrow entrances at small scale

In order to analyze the spatial distribution of *U. cordatus* burrows at a small scale, we produced maps of occupied burrows visible in the substrate of open non-rooted areas. Five maps, 1×3 m, were produced out of photographs of an identical area at five successive dates from December 2003 to January 2004. But because the number of points was relatively low for the statistical analysis (close to 20) an additional map of 3×5 m was done by direct mapping of another open area at the same elevation in October 2004. To observe the relation of burrow position with the positions of the surrounding prop roots (i.e., aerial roots of *R. mangle*), a 2×1 m map (enough in this plot to have >20 burrows and >20 roots) was produced of a *R. mangle*-rooted area where all burrow and prop-root positions were marked. All these maps were done in site RF, at locations of elevations above mean sea level >200 cm, and with a median size of burrow entrances <5 cm. These maps showed the X,Y position for each burrow entrance and prop root (for the second case) with a precision of ± 5 cm.

Spatial point pattern were analyzed using the univariate (distribution of burrows alone) or the bivariate (distribution of burrows according to position of roots) Ripley's K-function (Ripley 1977, 1981) to assess the random, clus-

tered or regular pattern of these positions. Considering two different types of events (1 and 2: in the bivariate case, root positions and burrow positions; in the univariate case only burrow positions), the K-function was calculated with the formula:

$$K_{1 \rightarrow 2}(r) = \frac{A}{n_1 \times n_2} \sum_{i=1}^{n_1} \omega_i(r) \sum_{j=1}^{n_2} \delta_{ij}(r) \quad (6.1)$$

where r was the radius of a circle where the density of points had to be considered; A was the entire area of the plot; n_1 and n_2 the number of points to be considered for type of event 1 and 2, respectively; $\omega(r)$ was a function of edge correction calculated from the density of type 2 on the area of radius r around the point i (of type 1); and $\delta(r)$ was a function returning 1 if the point j was at distance $\leq r$ of point i and 0 otherwise. The univariate adaptation of this function considered only one type of points (type 1 = type 2 = burrow positions, and always $j \neq i$). The precision of the r increment was considered as the field measurement precision (5 cm), and the maximum r was considered half of the smaller side of the plots. The K-function under a Poisson process distribution (or complete spatial randomness) should follow $\pi \cdot r^2$, and was therefore linearised to a more easily readable L-function (Discussion of Besag on Ripley 1977):

$$L_{1 \rightarrow 2}(r) = \sqrt{\frac{K_{1 \rightarrow 2}(r)}{\pi}} - r \quad (6.2)$$

For each analysis, a confidence envelope at 95% for complete spatial randomness (CSR) was calculated using the 2.5% and 97.5% quantiles of the L-function of 999 Monte Carlo randomization simulations. If the L-function values of the observed area were higher than this confidence envelope for a special radius (r) of measurement, clustering or attraction was considered at the scale of the corresponding radius. However, if the L-function values were lower than the confidence envelope, regularity or repulsion was considered at the scale of the corresponding radius.

6.3.4 Habitat heterogeneity effect on crab population at large scale

In order to analyze the potential effects of different variables on crab population structure at scales of several meters, three transects of 94 m, 59 m and 60 m were laid across mangrove forest areas in November 2004. Obviously, these three transects did not cover a representative sample of all the mangroves of the peninsula (213m² sampled against 140km² of mangroves

on the peninsula), but were selected non-randomly to cover an as wide as possible elevation range and two type of forest: *R. mangle*-dominated and *L. racemosa*-dominated. The first two transects were done at site RF in a frequently inundated area. The third transect was laid in a higher, less frequently flooded area at site LF. Along these transects, each 1 m² was taken as a sampling quadrat where the following measurements were done: number and size of occupied crab burrow entrances; surface elevation, root occupation, species of neighboring trees, and light availability. Measurements of crab burrows were done during low tide at neap tide so that we could see the maximum of burrows. The burrow entrance diameters were measured at the nearest cm. All burrows were opened down to 30 cm in the mud to confirm that only one burrow entrance was considered per crab. The additional entrances of a single individual were therefore discarded. To compare the three sites relative to mean sea level, surface elevation was measured with an optical level to the nearest cm, taking as reference fix tidal gauges. Two types of root occupation of the surface of the 1m² were considered: area occupied by *R. mangle* prop roots, and area occupied by other mangrove species (i.e., *Avicennia germinans* and *L. racemosa*) aerial roots, or pneumatophores. For *R. mangle*, we measured the percentage of the surface area occupied by *R. mangle* prop roots. Since *A. germinans* and *L. racemosa* have cable roots that run under the surface of the mud and the pneumatophores coming up the surface were too numerous to be measured, it was not possible to quantify the actual area that would influence where the crabs built their burrows. Thus, a qualitative measurement was attributed to each plot area according to the approximate proportion of area occupied by pneumatophores: 0 - no pneumatophores, 1 - less than ~1% occupied, 2 - between 1% and 5% occupied, 3 - more than 5% occupied. We used a qualitative measurement to describe the neighboring trees species in the surrounding 3m per 1 m² quadrat: 0 - when no tree trunks were found; 1 - when *A. germinans* was found or dominated; 2 - when *L. racemosa* was found or dominated; and 3 - when *R. mangle* was found or dominated. Light availability was measured with light sensors LI-190 (LI-COR inc.). Photosynthetically active radiation (PAR) was estimated around noon, on non-cloudy days, with three of these sensors in the middle and on two borders per 1 m² at 75cm above the ground. The mean PAR of these sensors was then compared to a sensor outside the canopy measuring PAR at the same time. These light measurements were used to characterize the canopy density directly above the quadrates, together with the shadow of big roots and trunks of the surrounding assumed to be preferred by *U. cordatus* (Rademaker unpublished manuscript).

The non-parametric Kruskal-Wallis analysis of variance (ANOVA) was used to analyze the effect of the two qualitative categorical variables (neigh-

boring species of tree, and pneumatophores importance) and the transect on the median burrow size and number of burrows.m⁻². A general regression model was constructed by forward stepwise selection of variables proposing the three continuous explanatory variables (i.e., percentage of *R. mangle* roots coverage, surface elevation above mean sea level, and percentage PAR reaching the soil surface) and their respective squares to explain the contiguous variances of median burrow size and number of burrows.m⁻².

6.3.5 Spatial distribution of burrow entrances at large scale

To analyze the patterns of spatial distribution of *U. cordatus* at large scale (tens of meters), we used the method of spatial pattern analysis along transects adapted by O'Driscoll (1998) from the K-function of Ripley to analyze the distributions of seabirds. This analysis considered transects of bins of measurement where each point within a bin was considered of distance B/2 (B being the size of the bin) to the other points within this bin. This approach worked only if the size of the bin was not smaller than the width of the transect. We considered the three transects described in the previous section separately, where each 1 m² was a bin of reading. All the burrows measured in these bins were assumed neighbors in the range of 0.5m. We conducted an univariate analysis to estimate the clustering of these burrows over large distances (up to half the length of the transects). Also, to estimate if a potential clustering of these burrows was due to the presence of *R. mangle* trees, each trunk of this species within the 1 m² was also considered for a bivariate analysis. The K-function was calculated with increments of r =1m with the simplified formula for one dimension:

$$K_{1 \rightarrow 2}(r) = \frac{1}{n_1 \times n_2} \sum_{i=1}^{n_1} \omega_i(r) \sum_{j=1}^{n_2} \delta_{ij}(r) \quad (6.3)$$

For the univariate analysis, n_1 was equal to n_2 and equal to the number of burrows measured along the entire transect (with always $j \neq i$). In the case of the bivariate analysis, the type 1 was the *R. mangle* trees, and type 2 was the burrows. For both cases, to evaluate the significance of the clustering at different scales, 999 Monte-Carlo randomizations of the burrow positions along the transects were generated. From these 999 simulations, the means $\hat{K}(r)$ of $K(r)$ were calculated. The function $L'(r)$ was calculated for the data sets and the 5th maximum values of the 999 simulations as:

$$L'_{1 \rightarrow 2}(r) = K_{1 \rightarrow 2}(r) - \hat{K}_{1 \rightarrow 2}(r) \quad (6.4)$$

If the $L'(r)$ of the data set was higher than the $L'(r)$ of the 5th maximum values, clustering or attraction could be considered at the r scale with a confidence of 95%.

All spatial analyses were conducted with algorithms prepared with the GNU-license R-software (version 2.2). Other statistical analyses were done with STATISTICA ©Statsoft (version 6.0).

6.4 Results

6.4.1 Burrows as proxy of crab population

The size of the 310 captured *U. cordatus* was significantly correlated to their burrow entrances (Fig. 6.1), which indicated that this variable could be used as a proxy of crab size.

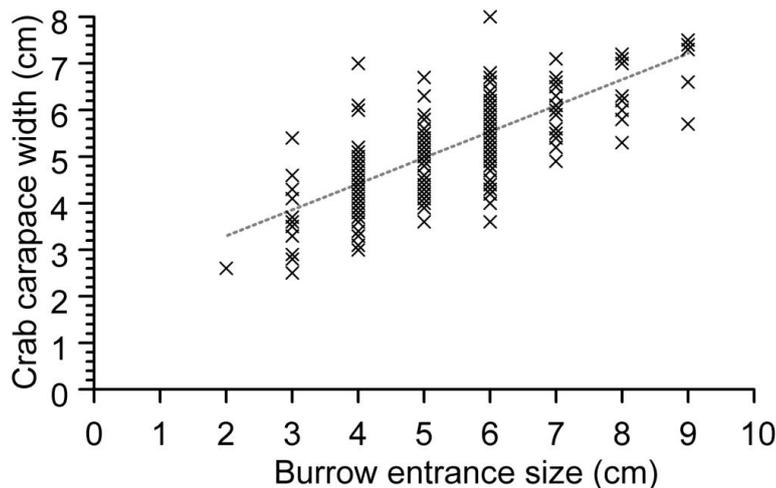


Figure 6.1: Relationship between sizes of 310 burrow entrances and sizes of *Ucides cordatus* captured in them. Samples made at neap tide in October-November 2003 on mangroves of the Caeté Peninsula (gray line represent the regression line, Spearman $R = 0.74$, Spearman Rank test $p < 0.01$).

6.4.2 Spatial distribution of burrow entrances at small scale

Non-rooted areas presented a regular spatial distribution of burrow entrances, with spacing around 25 cm (Fig. 6.2). The larger area gave a more significant regular pattern (Fig. 6.2g) than most of the smaller areas (Fig.

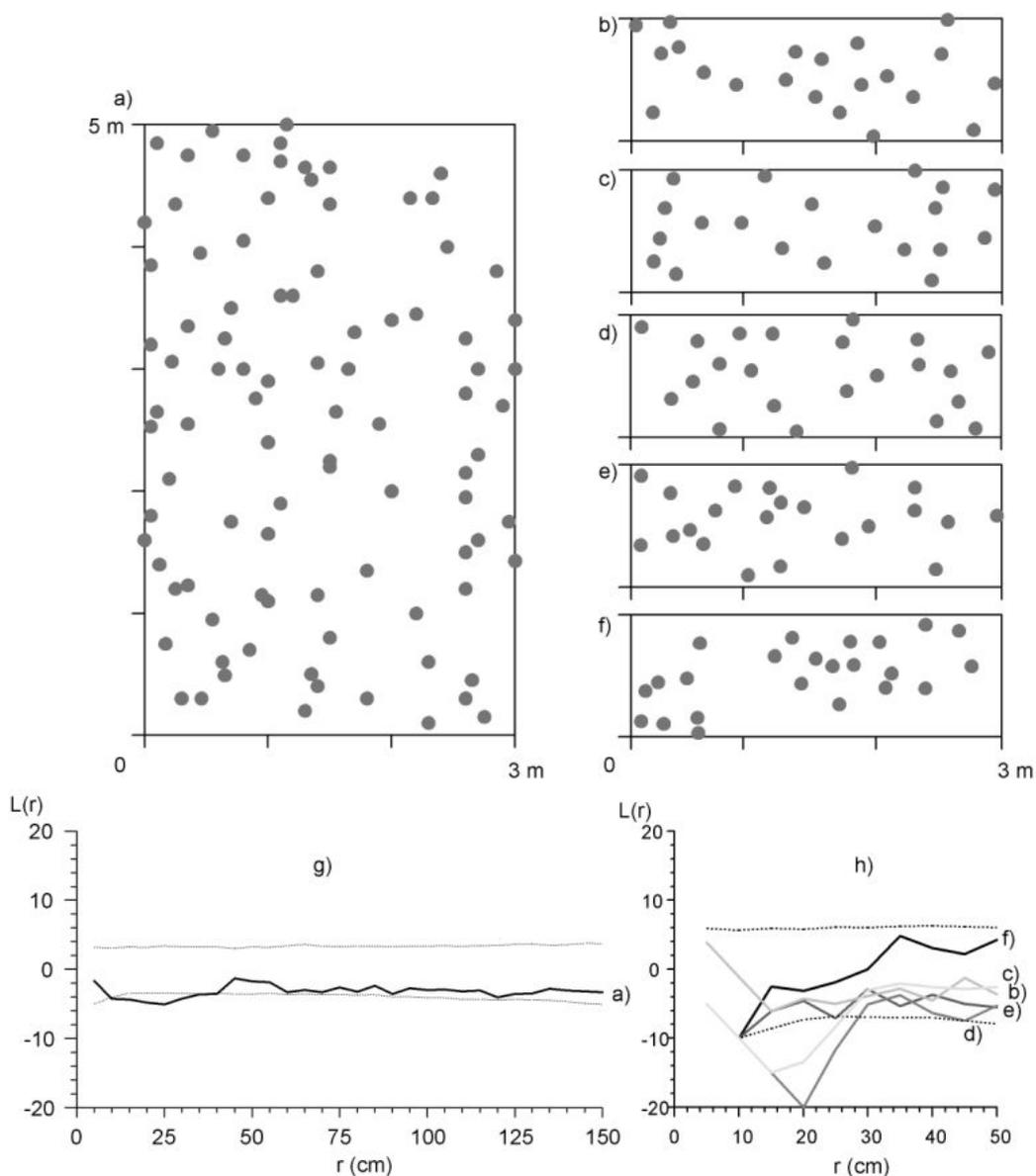


Figure 6.2: Spatial point pattern analysis of burrow entrances on non-rooted areas. a) area plotted the 27th of October 2004, b) to f) areas plotted from pictures taken between December 2003 and January 2004 of an identical area, g) Univariate L-function result of a), h) Univariate L-function result of b) to f). For g) and h) dashed lines represent 95% confidence envelope for complete spatial randomness (CSR) using 999 Monte Carlo randomizations.

6.2h), but 2 small plots (Fig. 6.2c and d) gave also a significant regular pattern around 20-25 cm of radius. These temporal variations in regularity of the pattern might be due to temporal differences of burrow use depending

on the tidal regime and crab activity. A regular pattern of burrows disposition was also observed around the same scale for the rooted area survey (Fig 6.3b). However, when the attraction of the roots for the burrows was considered, a clear clustering appeared at scale of 10 to 15 cm (Fig. 6.3c). Thus, *U. cordatus* preferentially created their burrow entrances closed to *R. mangle* prop roots. The crabs in this situation still kept a regular distance from each other.

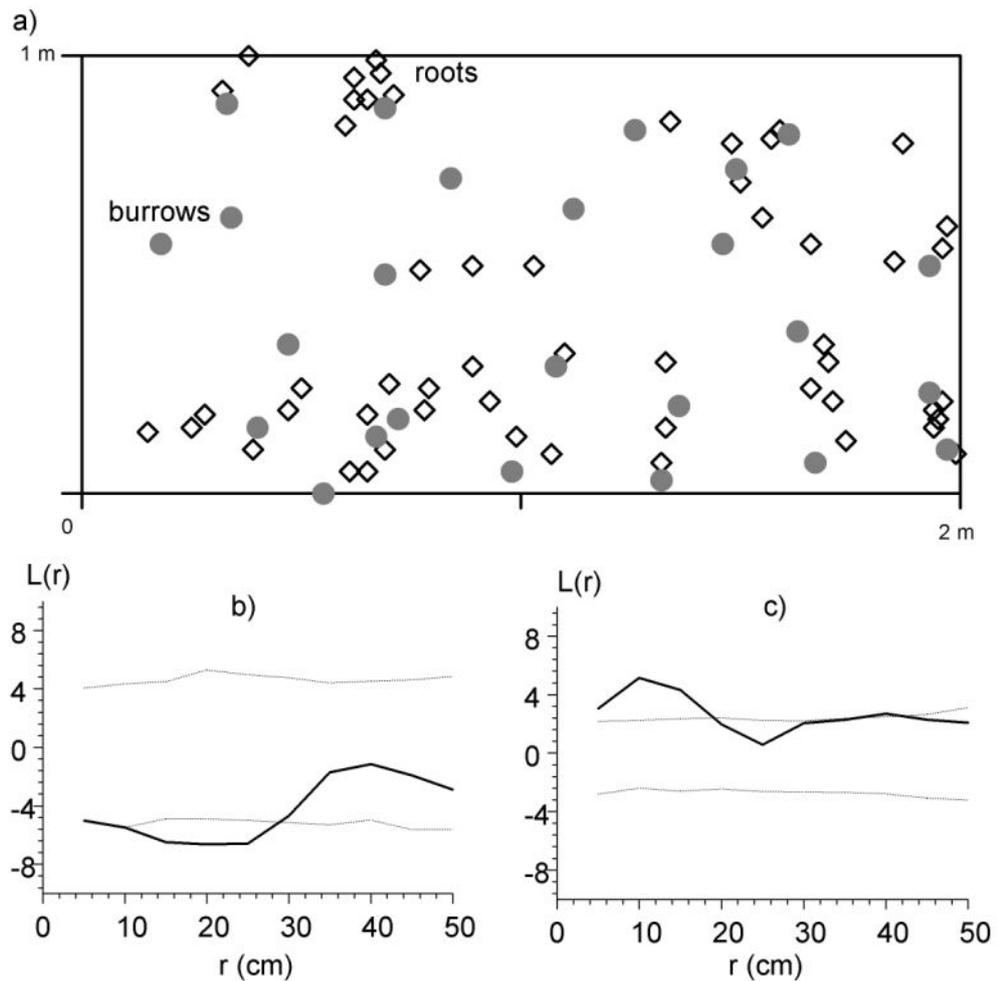


Figure 6.3: Spatial point pattern analysis of burrow entrances and prop root position on a *Rhizophora mangle* rooted area. a) area plotted the 8th of November 2004, b) Univariate L-function result for burrow positions c) Bivariate L-function result for burrow interaction with root position. For b) and c) dashed lines represent 95% confidence envelope for complete spatial randomness (CSR) using 999 Monte Carlo randomizations.

Table 6.1: Mean occupied burrow numbers and sizes of burrow entrance per transects. (* note that the median number of burrows and size per m^2 were used in the non-parametric statistical analysis, not the means)

Transect	Number of m^2 analysed	Mean* number of occupied burrows per m^2 (\pm SD)	Mean* size of burrow entrances (cm \pm SD)
1	94	6.44 \pm 3.21	6.02 \pm 1.89
2	59	4.68 \pm 2.20	4.93 \pm 1.89
3	60	6.93 \pm 2.84	4.23 \pm 1.58
All	213	6.09 \pm 2.99	5.21 \pm 1.96

6.4.3 Habitat heterogeneity effect on crab population

We found significant differences in burrow sizes and numbers among the three transects (Table 6.1, Kruskal-Wallis ANOVAs: $H(2, 213) = 56.291$, $p < 0.0001$; $H(2, 213) = 20.698$, $p < 0.001$, respectively). The third transect had smaller burrows and the second one had fewer of them. The effect of species of neighboring trees was also significant on size and number with generally more and bigger burrows close to *R. mangle* trees (Fig. 6.4, Kruskal-Wallis ANOVAs ($H(3,213) = 35.562$, $p < 0.0001$; $H(3,213) = 26.267$, $p < 0.0001$, respectively). The size and the numbers of crab burrows were

Burrow median size (cm)

or burrow number (/m²)

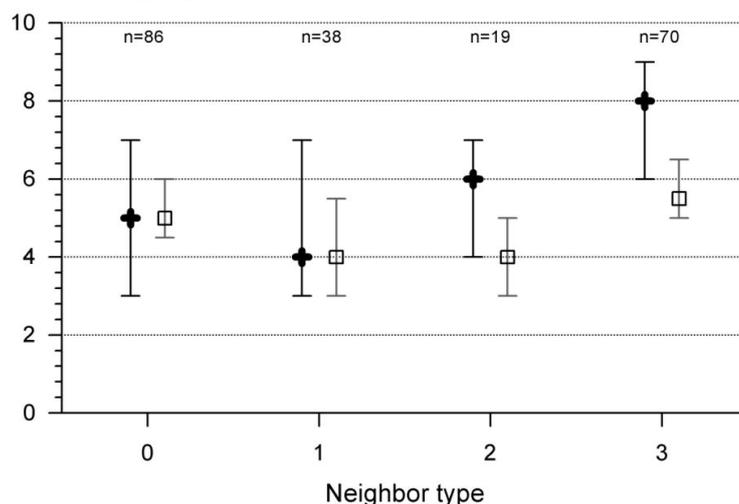


Figure 6.4: Number (crosses) and median size (boxes) of burrows depending on the neighboring tree species in the 3 m around (0: no trees, 1: *A. germinans* dominated, 2: *L. racemosa* dominated, 3: *R. mangle* dominated). Error bars represent first and third quartiles.

not larger with *Avicennia germinans* and *L. racemosa* trees in the neighborhood than without (Fig. 6.4). This was confirmed by negative relationships between burrow size and number against the qualitative variable of pneumatophores occupation (Fig. 6.5). The quadrats with the highest values of this variable were the ones with lowest numbers and smallest crab burrows.

Burrow median size (cm)

or burrow number (m^{-2})

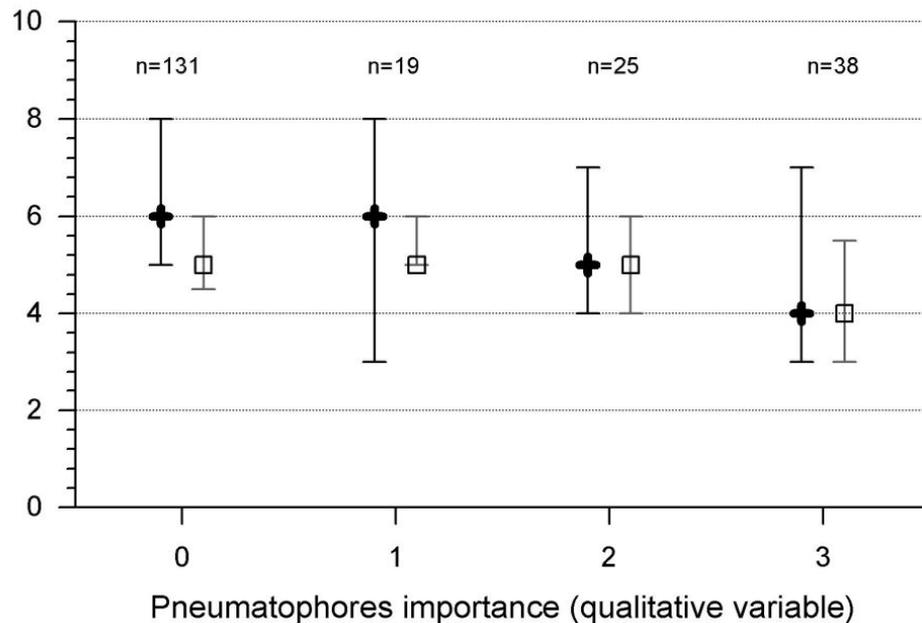


Figure 6.5: Number (crosses) and median size (boxes) of burrows depending on a qualitative description of pneumatophores occupations in the square meter of measurement (0: no pneumatophores, 1: less than $\sim 1\%$ occupied, 2: between 1% and 5% occupied, 3: more than 5% occupied). Error bars represent first and third quartiles.

Surface elevation was seen as related to burrow number and size (Fig. 6.6). Only quadrats above 150 cm of elevation had >9 burrows. m^{-2} . The quadrats with median burrow size >7 cm were in elevations between 150 and 200 cm above mean sea level. *Rhizophora mangle* prop roots occupation was also correlated to burrows since the quadrats with median burrow size >7 cm or >9 burrows. m^{-2} were always with *R. mangle* roots (Fig. 6.6). The PAR percentage reaching the ground had a less straightforward relationship, except that quadrats with median burrow size >7 cm or >9 burrows. m^{-2} were in highly lightened points (PAR% $>60\%$). The stepwise selection of the general regression model confirmed these trends (GRM, table 6.2). It

excluded the percentage of PAR but included elevation and *R. mangle* prop roots coverage as explanatory variables of median burrow size and number. Surface elevation was significantly correlated to burrow size but not to their number. Both explanatory variables had their square roots also included in the GRM with negative parameters, implying an optimal situation of size and number of burrows at intermediate elevation and coverage of *R. mangle* prop roots.

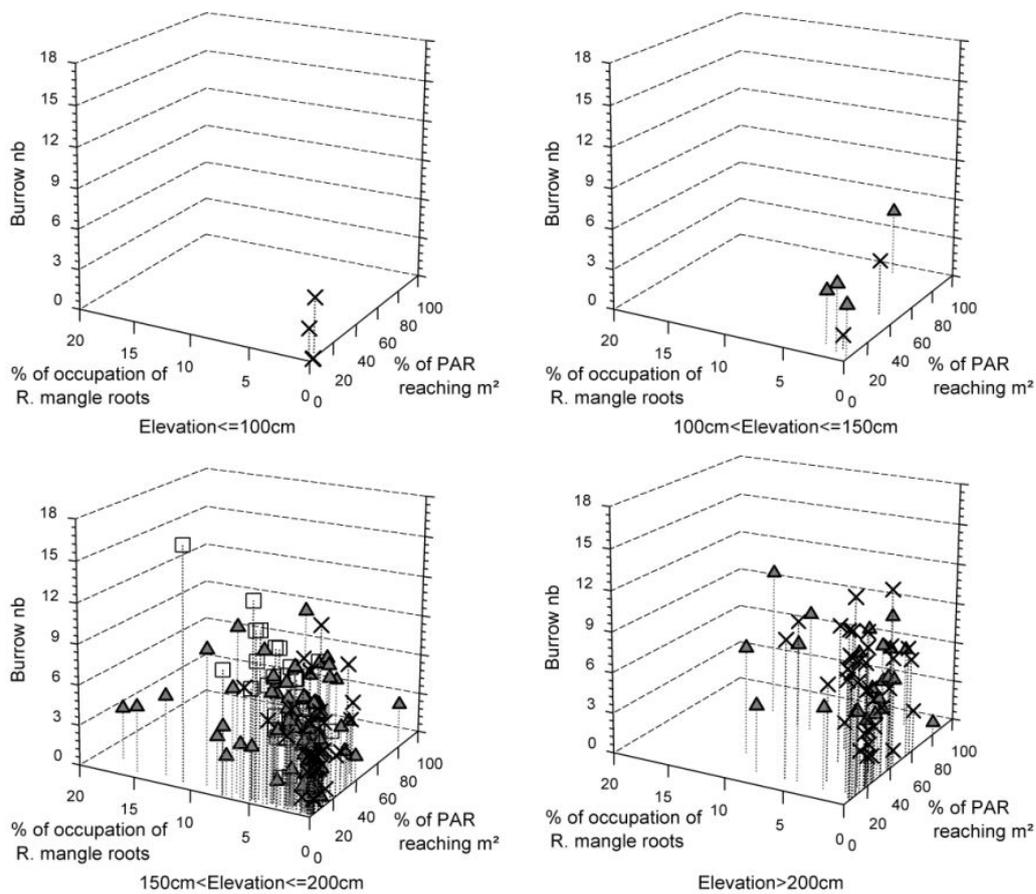


Figure 6.6: Number of burrows per square meter depending on the elevation, *R. mangle* prop root coverage and PAR percentage reaching the square meter measured. Median sizes of the burrows measured in each square meter are represented with the symbols: crosses $< 5\text{cm}$, $5\text{cm} < \text{triangles} < 7\text{cm}$, squares $> 7\text{cm}$.

Table 6.2: Results of General Regression Model with backward stepwise selection among the three continuous explanatory variables and their respective squares to explain the contiguous variation of number of burrows per square meters and median size of burrows. Last two columns show the respective parameters estimates in the GRM, bolded cases show significant influence at univariate level.

	F	Effect df	Error df	p	Parameter value for burrow number (\pm SE)	Parameter value for burrow median size (\pm SE)
Intercept	1.781	2	207	0.171	-0.0347 \pm 2.545	-2.194 \pm 1.16
Prop root % of occupation (R%)	28.953	2	207	0.000	0.822 \pm0.147	0.347 \pm0.067
Elevation (E) % of PAR reaching ground (PAR%)	24.758	2	207	0.000	0.036 \pm 0.03	0.094 \pm0.013
	pooled	0	-	-	-	-
$R\%^2$	15.593	2	207	0.000	-0.048 \pm0.0119	-0.021 \pm0.005
E^2	28.837	2	207	0.000	-4.6 e ⁻⁵ \pm 8.6 e ⁻⁵	-3.0 e⁻⁴ \pm3.9 e⁻⁵
$PAR\%^2$	pooled	0	-	-	-	-

6.4.4 Spatial distribution of burrow entrances at large scale

The three transects presented different trends of aggregation of *U. cordatus* burrows (Fig. 6.7). The first transect showed significant clustering of burrows at a scale between 2 and 15 m, with the highest significance around 10 m (Fig. 6.7b). The burrows were also significantly aggregated around the *R. mangle* trees with highest significance around a 5 m scale (Fig. 6.7c). The second transect presented only a very small significant clustering at scale of 3-4 m (Fig. 6.7e). However, the burrows were still significantly aggregated at a 5 m scale around the *R. mangle* trees (Fig 6.7f). Transect three, which was in a *L. racemosa*-dominated forest, still had some *R. mangle* trees present (Fig 6.7g). But, the burrows were not clustered at any scale (Fig. 6.7h), or around the *R. mangle* trees (Fig. 6.7i) along this transect. Thus, the presence of *R. mangle* seemed to drive an organization of *U. cordatus* at large scale in clusters around the trees, but only in forests dominated by this species.

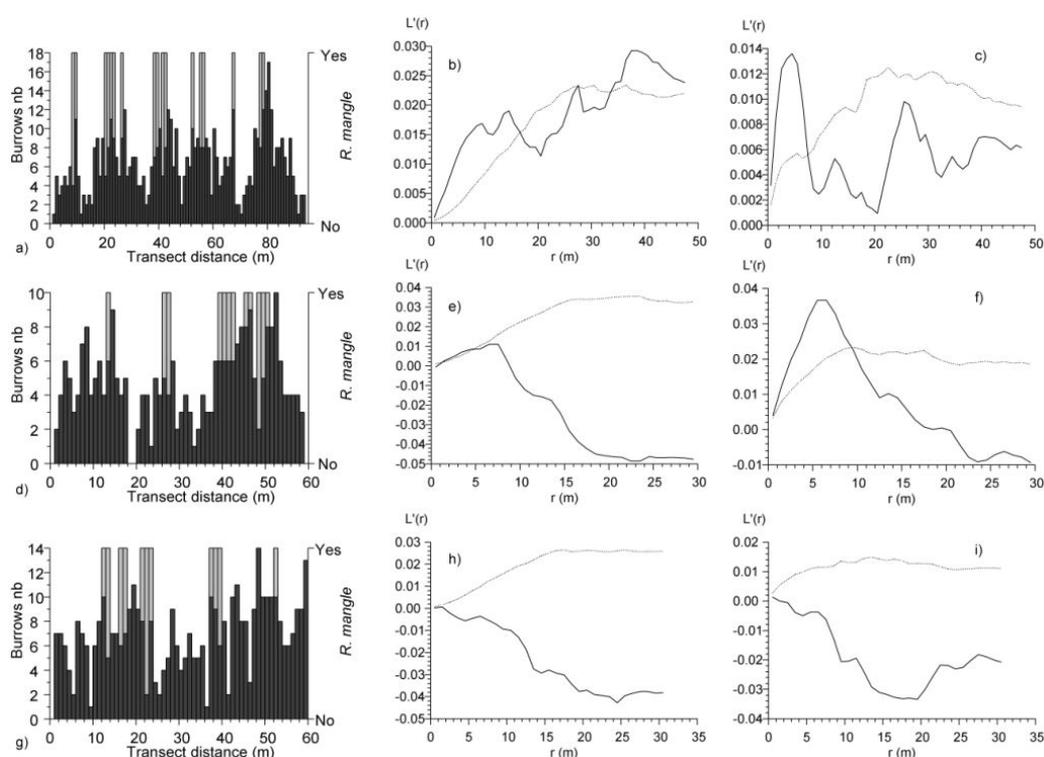


Figure 6.7: Spatial point pattern analysis of burrow entrances aggregation along the three transects (1: a-c; 2: d-f; 3: g-i; 1 and 2 are in a *R. mangle* dominated forests, 3 is in a *L. racemosa* dominated forest). Histograms a, d and g show the number of crabs per square meters along the transect (black bars), together with the occurrence of *R. mangle* trees (gray bars). Graphs b, e and h show the univariate analysis of clustering of burrows. Graphs c, f and i show the bivariate analysis of aggregation of burrows around *R. mangle* trees. For all graphs, the solid line represent the result of the transect data set and the dashed line represent the 95% confidence envelope calculated from 999 Monte Carlo randomizations.

6.5 Discussion

We analyzed the spatial organization of *U. cordatus* population on two mangrove sites of the Caeté Peninsula at different spatial scales and some potential factors explaining the distributions. At large scale, *U. cordatus* seemed to prefer clustering around *R. mangle* trees. The crabs preferentially built their burrows in intermediate rooted areas and intermediate elevation areas, where, in general, the big crabs dominated and probably excluded smaller individuals to secondary areas. Although *U. cordatus* individuals aggregated themselves in these rooted areas at a large scale and close to the roots at a small scale, our observations indicated that a repulsion process probably due to intraspecific competition for food organizes the crabs in a

regular pattern at small scale.

Crab densities estimated in our study were much higher than reported in previous work done on these areas. The difference was clearly due to the sampling design. Two factors might have played an important role on that. Schories et al. (2003), Diele et al. (2005), and Nordhaus et al. (2006) estimated population density during spring ebb tides and by fishing the crabs. Although they sometimes considered unfished crabs in their density calculations, they never reached density values as high as ours. Our method of sampling by counting and opening burrows could also be criticized, but, the major difference was actually due to crab behavior at the sampling times (i.e., spring vs. neap tide). Specifically, most of the small crabs close their burrows before spring tides (K. Diele & C. Piou, personal observations). The closed burrow entrances are generally over-washed by the tide and therefore not visible at ebb tide. Thus, even with the burrows not fished included in their density calculations, the previous studies probably missed many of the small crabs. The second factor might be the fact that we focused voluntarily on densely populated areas. The previous studies sampled more randomly, covering therefore also areas of the peninsula of really low crab density (such as channels or dry land). The mean density of these studies is therefore probably an overall better estimate for the peninsula than the one we could have drawn from the 213m² covered in our study. However, with these high densities found on the *R. mangle*-dominated forest and regenerating *L. racemosa*-dominated forest, the litter-processing roles of *U. cordatus* documented by Schories et al. (2003) and Nordhaus et al. (2006) is higher than previously assumed. Identically, the food limitation calculated by Nordhaus (2004) might have more effect than expected in our *R. mangle*-dominated site (also place of Nordhaus work).

Because of this food limitation, competition for food can be proposed to be the main factor driving the spatial distribution of the crabs at small scale. The typical leaf-harvesting behavior of *U. cordatus* is an indicator of this high intraspecific competition. For example, when a *R. mangle* leaf falls on the mangrove forest floor, *U. cordatus* will move slowly towards it and grab it. The first crab to get the leaf will pull it quickly into its burrow to eat at some later time (Nordhaus 2004, C. Piou personal observation). These observations indicate how important it might be for the crabs to distribute in a relatively regular pattern on the muddy surface so that the opportunities for leaves are evenly dispersed. Nordhaus (2004) also demonstrated that *U. cordatus* fed on mangrove mud more than 30% of the time, probably looking after microphytobenthos to compensate the high C:N ratio of mangrove leaves as Steinke et al. (1993) suggested for a sesarmid crab. *Ucides cordatus* often dig out large amounts of anoxic mud from their burrows. This behavior may

be linked to the care of the burrow structure, but might also be associated with mud feeding. With the asperities created in the substrate, the crabs thus increased the total surface area of the mud surrounding their burrows and provided more space for microphytobenthos to develop. Thus, the regular spatial distribution of the burrows could also be the result of competition for space for microphytobenthos. Competition for space can lead to movement of change of burrow as proposed by Chapter 7 in a modeling study. And another factor that may be involved in this small-scale, regular distribution is the capacity of *U. cordatus* to move its burrow entrance. Each time a crab closed its burrow, it could move the next opening of up to 10cm (C. D'Lima, C. Piou personal observations). When entrances of adjacent burrows get too close, a crab can move its entrance and thereby decrease direct spatial competition.

We also observed this small-scale, regular distribution in rooted areas, but the crabs preferred to install their burrow entrances close to the prop roots of *R. mangle* trees. Several factors might explain this pattern. First, a burrow close to a prop root has more stability and might be easier to maintain on very soft mud such as the sediment of the frequently inundated mangroves of the Caeté Peninsula. Second, roots also produce a shelter against predators such as mangrove raccoon (*Procyon cancrivorus*), monkeys (e.g. *Cebus apella*) or humans who fish the crabs by pulling them out of their burrows. Rooted areas are obviously harder if not impossible to access and fish than unvegetated areas. Finally, the bottoms of prop roots, which are covered in mud and algae, are sometimes fed on by *U. cordatus* (C. Piou personal observation). Thus, this might be another feeding advantage for the crabs to install their burrows close to roots.

The feeding habits and spatial competition of *U. cordatus* can be transferred to the larger scale to explain some part of the habitat preference described by the transect study. We found that there were more and larger *U. cordatus* associated with intermediate rooted and elevated areas. *Ucides cordatus* feeding preference for *R. mangle* leaves (Nordhaus, 2004) may explain why they generally install their burrows close to this species. These findings are concordant with the observations of Diele et al. (2005) and Nordhaus et al. (2006) who propose that the preference for *R. mangle* prop root zone offers protection against predation. The other two mangrove species do not provide this shelter, and generally grow at higher (thus harder sediment) or lower elevation than the *R. mangle*. However, high *R. mangle* root densities close to the trunk of the tree might reduce the available space for sediment to settle. To our knowledge, no studies have ever tried to quantify differences of leaf litter according to the distance of the trunk, but it seems likely that the leaves will not fall directly beneath the trunk where the root density is gener-

ally the highest. For the surface elevation preference, we saw that *U. cordatus* favored an intermediate situation. At high elevations where they are flooded less frequently by the tide, they cannot refresh their gills as frequently (C. Piou personal observation). They also have less access to microphytobenthos production at high elevations. At low elevations, frequent inundations reduce the number of hours available for harvesting falling leaves. Thus, the intermediate elevations provide optimal conditions for leaf litter availability, microphytobenthos production and physiological preferences.

However, we have seen that *U. cordatus* also occurs in habitats other than *R. mangle*-dominated forests. These are generally smaller crabs, in concordance with observations of Diele et al. (2005), and are probably the result of competitive exclusion from their preferred habitats. *Ucides cordatus* is a very slow growing crab, reaching 6 cm carapace width at >4 yr (Diele 2000, Pinheiro et al. 2005). The density of small compared to big individuals in the preferred habitats defined above is too low to assume a growth within the same burrow for the entire life of a crab. Movement, which has to occur, was also demonstrated in Chapter 7 as the result of intraspecific competition at individual level. The population repartition of small crabs in adjacent habitats and big crabs in preferred habitats could consequently be the result of asymmetric competition where a few big crabs can exclude several small crabs from an area.

We also demonstrated that the crabs aggregated around *R. mangle* trees at a large scale in areas dominated by this species. Although we assumed it was their preferred habitat, they do not show a clustering around *R. mangle* in a *L. racemosa*-dominated forest. There are two possible reasons for this pattern. First, the two transects in our study that showed clustering around *R. mangle* trees also had relatively larger burrow entrances and therefore bigger crabs than in the *L. racemosa* forest. These smaller and more numerous crabs might have been excluded from beneath the *R. mangle* trees in the *L. racemosa* forest and thus the clustering is not apparent in this transect. Second, the *L. racemosa* forest was at a higher elevation than the other two transects. Thus, the sediment was harder even beneath *R. mangle* trees. Additionally, the *L. racemosa* forest was relatively young forest because it was in a state of recovery following perturbation by a road construction across the peninsula (Berger et al. 1999). The hardness of the sediment and the previous disturbance to the site might have resulted in a lower frequency of predation than in the tall *R. mangle* forests. The advantages of stability of the sediment and shelter against predation provided by proximity to *R. mangle* roots were not apparent in this situation, and the crabs had fewer reasons to prefer the rooted areas. This suggests that the only other reason for the crabs to prefer the *R. mangle* rooted areas is the feeding preference of

U. cordatus for *R. mangle* leaves (Nordhaus 2004). However, this preference was never tested for crabs from *L. racemosa*-dominated forests, and could therefore be different for crabs of these forests.

Differences in organization patterns at different scale is typical of burrowing organisms and has been demonstrated for kangaroo rats in North American deserts (Schooley & Wiens 2001) or earthworm species in an African grass savanna (Rossi 2003a). The influences of the habitat heterogeneity on distribution patterns were also seen for these earthworm species (Rossi 2003b) and for other earthworms in a Colombian pasture (Decaëns & Rossi 2001). In our case, we found that the organization of *U. cordatus* population at large scale is in response to habitat heterogeneity. However, competition for food, which occurs at the individual level, probably also influences the distribution of *U. cordatus* at large scale. These observations can help in defining a preferred habitat type as a highly productive *R. mangle*-dominated forest, at intermediate prop root occupation and surface elevation conditions. To address the question posed by Nordhaus et al. (2006) regarding the reasons of lack of importance of *U. cordatus* in other Neotropical mangroves, our study provides a first documentation for the definition of preferred habitat and the observed transfer of influence of the feeding and other individual behaviors from small to large scale. On a biogeographic scale, this transfer of information obviously does not depend only on individual behavior because factors such as interspecific competition and larval dispersal might also play important roles. However, the quality of the habitat as a food source for this species is still important. Consequently, we expect that places where large *U. cordatus* populations develop would not be mangrove forests with dominance of *A. germinans* or *L. racemosa*, low litter production, infrequent or too frequent flooding, or other conditions such as different substrate types or competing leaf-eating animals on the mangrove floor. Finally, to support this hypothesis of preferred habitats, *U. cordatus* populations should be estimated, spatially investigated and their roles in the litter processing analyzed in many other Neotropical mangroves. In particular, these investigations should focus on large contiguous Neotropical mangrove ecosystems with fine silty sediment and highly productive forests dominated by *Rhizophora spp*, where we would expect high importance of *U. cordatus*. In such environments, it is important to determine which of the two ecosystem engineers, *R. mangle* or *U. cordatus*, is first to recolonize in gap areas, and whether *U. cordatus* influences the patterns of vegetation zonation as proposed for grapsid crabs in Indo-Pacific mangroves (Smith 1987).

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Chapter 7

Simulating cryptic movements of a mangrove crab: recovery phenomena after small scale fishery



Simulating cryptic movements of a mangrove crab: recovery phenomena after small scale fishery

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7.1 Abstract

The semi-terrestrial burrowing crab *Ucides cordatus* is an important ecological component and economic resource of Brazilian mangrove forests. The crab population of the Caeté peninsula (the location of our study sites) has been exploited for the last 40 years. Recovery of fished areas by crabs from non-fished areas under the roots of the mangrove tree *Rhizophora mangle* was hypothesized to be an important buffer mechanism against rapid over-fishing. However, catch per unit effort decreased in recent years, suggesting that the sustainability of the crab fishery might become endangered. It is therefore important to better understand the movement behaviour of these crabs, even though it is hard to observe directly. Following the approach of pattern-oriented modelling, we developed an individual-based model to infer movement behaviour from patterns in density recovery that were observed in field experiments. Two alternative submodels simulating factors causing movement were contrasted: with and without local competition among crabs. To describe local competition, the field-of-neighbourhood (FON) approach was used, which was originally designed for sessile organisms. Without com-

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petition, unrealistically high movement frequencies were required to fit the observed linear recovery patterns. With competition included, better fits to the recovery patterns were obtained, and lower and thus more realistic movement frequencies were sufficient. This indicates that local competition between crabs is the main reason for them to move and change their burrows. Our work shows that the FON approach is suitable to describe local interactions not only among sessile organisms, but also among mobile organisms in conditions of competition for resources. The simulation results illustrate the importance of the non-fished rooted areas as buffers against rapid over-fishing. The IBU model presents a potential for future analysis of these buffer mechanisms and thus for a better understanding of the crab fishery and its management.

Key Words: *Ucides cordatus*, individual-based model, field of neighborhood, pattern-oriented modeling, local competition, movement.

7.2 Introduction

The semi-terrestrial crab *Ucides cordatus cordatus* (Linnaeus 1763) (hereafter referred to as *Ucides cordatus*) is an important ecological component (Branco, 1993; Blankenstejn et al., 1997; Wolff et al., 2000; Koch and Wolff, 2002; Schories et al., 2003; Nordhaus et al., 2006) and economic resource of Brazilian mangrove forests (Glaser, 2003). Fisheries on this crab have been reported from many places of Brazil (e.g. Alcantara-Filho, 1978; Nordi, 1994a, b; Alves et al., 2005), and catches can reach very high values, up to $\sim 8.0 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the Caeté peninsula, where our study was carried out (Diele, 2000; A.-R. Araujo, *unpublished data*). The Caeté peninsula is covered by 140 km² of mangroves and is located 200 km east-north-east of Belém. It was the focus area of a long-term interdisciplinary research project on sustainable coastal management (MADAM project; Berger et al., 1999) including work on the biology of *U. cordatus* (Diele, 2000; Nordhaus, 2004; Diele et al., 2005; Diele and Simith, 2006; Nordhaus et al., 2006).

The local crab population has been exploited for 40 years, but to date, crab collectors mainly employ non-destructive, artisanal capture techniques by using their bare arm or a hooked stick to pull the crabs out of their burrows (Glaser and Diele, 2004). Mainly mature large males are harvested, and crab collectors report recovery of fished areas in less than two weeks (Diele et al., 2005; C. Piou, *personal observation*). So far, the traditional fishing techniques do not seem to have affected the biological sustainability of the Caeté crab population (Diele et al., 2005). However, 6 and 8% decreases in

catch per unit effort occurred in 1999 and 2000, respectively (stable values thereafter) (Diele et al., 2005), suggesting that the economic and social sustainability of the crab fishery in this area might become endangered (Glaser and Diele, 2004).

The recovery of the fished areas is not yet fully understood and the factors influencing it at the individual level are not known. *Ucides cordatus* grows very slowly and reaches maturity after ~ 2.5 years and fishing size (usually > 6.5 cm carapace width) only after 7 years (Diele, 2000). This shows that the specimens that restock fished areas are not recently settled young recruits, as believed by crab collectors. The additional fact that large (i.e. old) and small (i.e. young) crabs are usually not found in same densities in the mangrove forest (e.g. Diele et al., 2005) indirectly indicates movement. Finally, one important buffer mechanism leading to recovery of fished areas is believed to be the movement of crabs from non-fished areas to fished ones. In *Rhizophora mangle* forests, the most important fishing grounds, non-fished areas are patches of dense roots, which are inaccessible to the fishermen (Diele et al., 2005). Forests dominated by *Avicennia germinans* and *Laguncularia racemosa* are less frequently fished because root carpets and/or sandy substrate hamper fishery. Both types, non-fished and less fished areas, might function as buffers at different spatial scales. However, in *A. germinans* forests, crab density and average size is much lower than in *R. mangle* dominated forests (Diele, 2000).

So far, only scarce information could be collected on individual movement behaviour. Crabs moving long distances and searching where to establish a new burrow were only very scarcely seen in a total of many dozens of full day observations. Nordhaus (2004) investigated the behaviour of *U. cordatus* near their burrows and found that most crabs remain quasi immobile in or nearby their burrow entrances. She quantified their short-distance movements around the burrows for foraging on mangrove leaf litter (during 0.3% of the time and with maximum distance of ~ 1 m), but could not estimate how often crabs change burrows and to what distance new burrows are built or overtaken. Nevertheless, an important conclusion made by Nordhaus et al. (2006) is that the *U. cordatus* population at the Caeté peninsula is food limited. This becomes obvious from the fact that *U. cordatus* usually completely depletes the leaf litter from the floor of *Rhizophora mangle* forests.

The purpose of this study was to understand the behaviour of *U. cordatus* crabs that promotes the recovery of fished areas on a small scales (< 1 ha) in *Rhizophora mangle* forests. We tried to quantify this recovery pattern and the movement of crabs in the field. We developed an individual-based model of the crabs and their behaviour and followed the idea of pattern-

oriented modelling (Grimm et al., 1996; Grimm and Berger, 2003; Wiegand et al., 2003; Grimm et al., 2005) that patterns at the system level contain information about processes at the individual level. We thus formulated alternative sub-models, or theories (Grimm and Railsback, 2005), of movement behaviour and checked how well they were able to reproduce recovery patterns observed at the population level.

One of our main questions regarding the movement of crabs was to understand what forces them to give up a burrow in the first place and to establish themselves in a new area, e.g. a fished one. We tested whether competition among crabs for food as documented by Nordhaus et al. (2006) could be the trigger for crab movement. In the following, we describe the patterns observed in the field, the Individual-Based-*Ucides* (IBU) model and its submodels, and finally show the assumptions under which IBU best fits the observed recovery patterns.

7.3 Field experiments

7.3.1 Methods

To study the recovery of fished areas on a small scales ($<1\text{ha}$), field experiments were conducted in a mangrove forest dominated by tall *Rhizophora mangle* trees in the northern part of the Caeté peninsula, close to the tidal channel, Furo Grande ($0^{\circ}50'15''\text{S}$ and $46^{\circ}38'30''\text{W}$). Although not according to the fishing methods applied by local crab collectors, two experiments of complete exclusion of crabs from areas of high density of crabs ($>4\text{m}^{-2}$) without roots were conducted in November-December 2003 and 2004. The proportions of closed burrows versus open burrows as well as occupied burrows versus non-occupied burrows were estimated before the experiments started. In the first year, one plot of 12.25 m^2 was fished entirely and the mud flattened to remove the signs of fishery and burrow entrances (hereafter referred to as experiment 1). In the second year, 6 plots of the same size were fished entirely but the burrow entrances and the holes created by the crab collector were left accessible for re-colonization (experiment 2). The numbers of active burrows, indicating the number of returning crabs, were determined for 50 days in experiment 1 and for only 15 days in experiment 2 because of a sampling hazard. The ratio of number of occupied burrows after fishery to the original number before fishery was taken as an indicator for re-colonization.

Additionally, 9 plots of 3m^2 covering a more diverse type of habitat (in elevation and root density) as well as data from Diele (2000) and data from

transect sampling (Piou et al., *unpublished data*) were used to estimate proportions of burrow occupation and status (closed or open) and to estimate mean crab density and related size.

To enhance the knowledge on *U. cordatus* behaviour, we also observed individual specimens in the field. *Ucides cordatus* can spend several days in its burrow without coming out and blocks its entrance with a plug of mud. We followed the burrow status of >100 crabs during 2 to 5 weeks to obtain estimations on how often burrows were closed and for how long. In 2003 and 2004 several tagging-observation experiments were performed (in total 98 individuals tagged) to evaluate the frequency of burrow change and distances covered when crabs change their burrow. Tagging methods included radio-tracking, paint or other visual marks fixed on the back of the carapace of individuals.

7.3.2 Results

For the areas of the two recovery experiments, mean burrow density before fishery was 5.29 ± 0.97 burrow.m⁻². After fishery, recovery was faster when leaving holes on the ground surface (2004, experiment 2) than after flattening (2003, experiment 1) (Fig. 7.1). Comparing the first day after fishery in the two experiments, recovery was higher in experiment 2 because existing burrows could immediately be colonized. We found linear correlations between the proportion of occupied burrows found on the plot (F) and the number of days after fishery (t) for the two experiments:

$$\begin{aligned}
 F(t)_{2003} &= 0.0056 + 0.0189t \\
 \text{and} & \\
 F(t)_{2004} &= 0.2568 + 0.0287t
 \end{aligned}
 \tag{7.1}$$

with R^2 of 0.99 and 0.71 respectively. These regression formulas were taken as the main patterns of linear recovery to be reproduced by the IBU model.

In general, in forests dominated by *Rhizophora mangle*, mean crab carapace size was 6.05 ± 0.9 cm with mean density of 3.16 crab.m⁻². The proportion of closed burrows was measured as at least 60%, while the unoccupied burrow proportion was about 20%. Both proportions varied in space and depended on the tidal cycle.

None of the methods of following the crabs' movements in the field was entirely successful because crabs were generally not re-observed after release. We obtained rough estimates of the frequency of movement from >0 to 0.15 move/crab/day and a mean walking distance between 0.2 and 50 m/day. Furthermore, our field observations showed that on average crabs closed their

burrows once a week and that the burrows remained closed for a mean period of about 3 days.

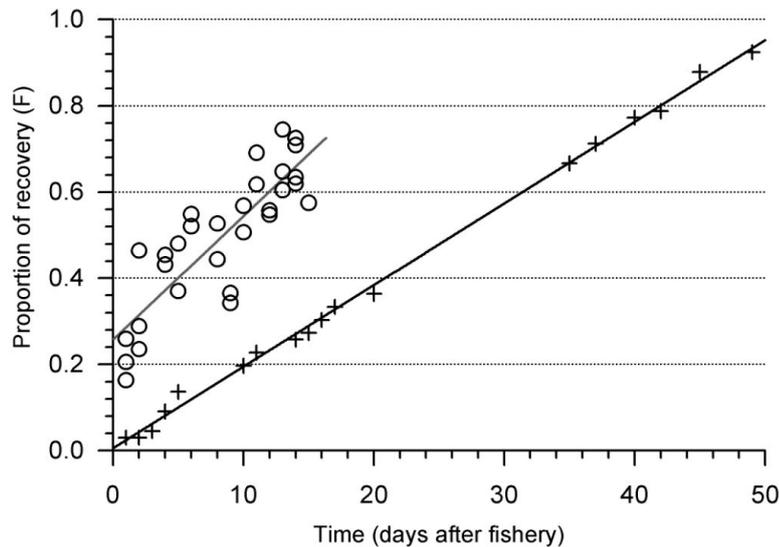


Figure 7.1: Proportion of occupied burrows through time after the fishing experiment, flattening the surface in 2003 (experiment 1: crosses) and leaving the holes in 2004 (experiment 2: circles) with respective regression lines.

7.4 The IBU model

7.4.1 Description

The following model description follows the ODD protocol for describing individual- and agent-based models (Grimm and Railsback, 2005; Grimm et al., 2006) and consists of seven elements. The first three elements provide an overview, the fourth element explains general concepts underlying the model's design, and the remaining three elements provide details.

Purpose

The main purpose of the IBU model was to reproduce the patterns of recovery of the crab population after fishery at small scales (<1ha). It was tested whether local competition among neighbouring crabs is a reasonable explanation for the crabs' movement.

Structure, scales and states variables

The simulated area corresponded to a homogeneous mangrove mud flat of 15×15 m with a square fished area in the center of 12.25 m^2 . The area had periodic boundaries (=Torus), so that the number of crabs was constant throughout the simulation. The temporal unit was one day.

The state variables of individual crabs were: identity number, position, carapace width (CW), angle of direction of movement, and identity number of occupied burrow. The burrows state variables were: identity number, position, hosted crab id (if any), open/close status and time without a crab (if not occupied, t_{empty}).

Process overview and scheduling

During each time step, the following sequence of processes was simulated: updating of parameters of the submodels that describe the interactions among the crabs, checking the status of all burrows with removing those that were empty for too long time (see submodels), and checking the status of all crabs in a random order. During this last process, individual crabs could accomplish one of the following actions: do nothing; change the open/close status of its burrow; or leave its burrow (if it was open) and take over or create a new one. The movement of a crab consisted of different subprocesses: reason for moving, walking behaviour and reason for stopping, which determined three modules described in the submodels section.

Design concepts

Emergence. - Recovery of entirely fished areas emerges from the behaviour of the individual crabs and, in particular, from their interactions via local competition.

Interaction. - For crabs in their burrows, two assumptions of competition interactions influencing their reason of movement were tested: no apparent interactions (Null assumption); and competition with neighbouring individuals for shared resources (Field Of Neighbourhood or FON assumption). Food resources (mangrove leaves fallen from the trees) for which *U. cordatus* compete, are assumed as continuously renewed and homogeneous on the mangrove floor. However, the competition intensity for these leaves depends on their distance from the burrow entrance and, probably, on the size of the involved individuals. Thus, we adapted the Field Of Neighbourhood (FON) approach to describe competition (Berger and Hildenbrandt, 2000; 2003). The FON approach assumes a circular intensity field around each crab representing its harvest area. Crabs were considered to interact if

their fields overlapped. Distance and size of the neighbours determined the intensity of their FON effect on a given crab. The sum of the FON effects was assumed to influence the probability of leaving a burrow. Therefore, this approach implicitly assumed an effect of food limitation on the crabs' movement (Nordhaus et al., 2006).

Stochasticity. - Most elements of individual crab behaviour (such as closing/opening its burrow, taking over a burrow, and reason, direction or the stopping of movement for some submodels) and burrow disappearance were ruled by empirically determined probabilities (Table 7.1). Stochasticity was used for each of these probabilities. This accounted for individual variability and the fact that detailed lower level information on processes determining these behaviors is not available.

Observation. - Information about crabs and burrows could be obtained at each time step with a graphical user interface including a map of burrows, crabs, fields of neighborhoods, and movement paths (Fig. 7.2). This interface was used for model testing and visual debugging (Grimm, 2002). Numerical outputs were used for further analyses.

Initialization

IBU simulations were initialized by first creating the number of crabs given by the input density (Dc) together with their burrows in random position in the area; and secondly by adding the proportion ($PropUnoc$) of unoccupied burrows at random positions. The open/closed status of all the burrows was determined randomly following a probability corresponding to expected proportion ($PropClosed$). These last two proportions were given as input from field observation. Carapace size of individual crabs was randomly attributed according to a normal distribution with a given mean size (CW_{pop}) and standard deviation ($SD_{CW_{pop}}$) for the simulated population (see Table 7.1 for all these parameters). After assigning these initial states, simulations were run for ten days in order to establish a typical situation caused by the crabs' interactions. Tests showed that ten days were sufficient for this. Then, fishing was simulated in the central fishing area by removing all crabs and also removing or not removing the burrows, to simulate the two field experiments respectively (see description of experiment 1 and 2 above, and model analysis below).

Input

Environmental conditions were assumed to remain constant during the simulation experiment, so no input was required after the initialization phase.

Table 7.1: Parameters and initialization values for the IBU model. Sources: (1) Compilation of data from Diele (2000) and additional measurements on population structure; (2) Estimation from individual behaviour of Nordhaus (2004); (3) Estimation from experiments on individual crab behaviour.

Parameter name	Description	Initial values	Assumptions	Source
Dc	Crab starting density (in /m ²)	3.16	Homogeneous area that does not consider habitat heterogeneity	(1)
$PropUnoc$	Proportion of unoccupied burrows at start	22%	Neap tide situation	(1)
$PropClosed$	Proportion of closed burrows at start	60%	-	(1)
CW_{pop}	Mean carapace size of the simulated crab population (in cm)	6	Few fished-size crabs and more smaller ones	(1)
$SD_{CW_{pop}}$	Standard deviation of the mean carapace size of the simulated crab population (in cm)	1	-	(1)
a and b	Constants for the interaction radius calculation (Eq. 7.2)	19 and 15cm	For a crab of $CW=1$ cm $R_{int}=24.5$ cm, and above $CW=9$ cm all crabs $R_{int}=100$ cm	(2)
P_{c1}	Probability of taking over an occupied burrow	0.0	Impossible	(3)
P_{c2}	Probability of taking over a closed empty burrow	0.25	Possible if pass just on top	(3)
P_{c3}	Probability of taking over an open empty burrow	1.0	Would always prefer to stop if find an open empty burrow	(3)
$P_{closing}$	Probability that a crab closes its burrow at each time step	0.14	Close its burrow \sim once a week	(3)
$P_{opening}$	Once closed, probability of opening its burrow at each time step	0.33	Closing period of \sim 3days	(3)

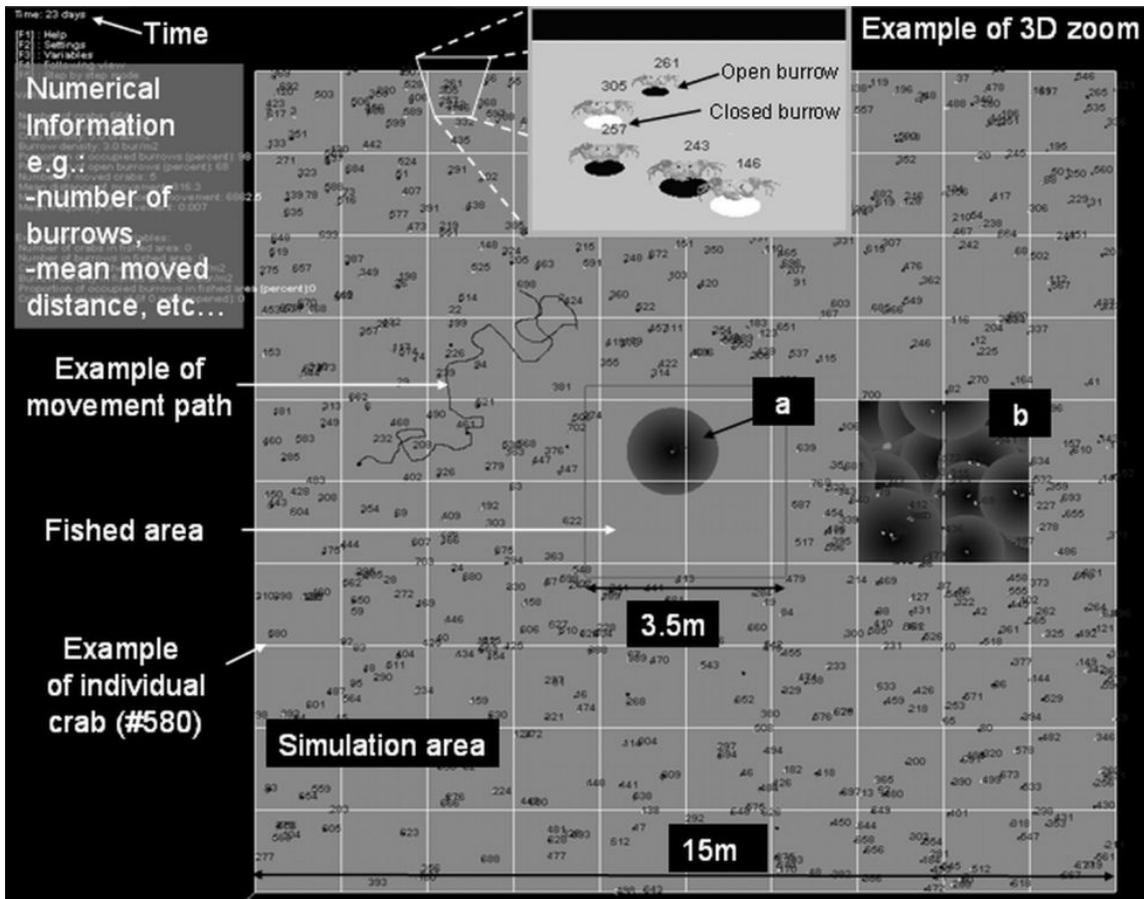


Figure 7.2: Snapshot of IBU model interface with examples of particular features related to the fishing experiment and the field of neighborhood (FON) interaction submodel (a: single crab FON area, b: example of an area of interactions with visualization of FON areas of all crabs)

Submodels

Dispersal of crabs was described as a combination of three modules: Reason for movement (RM), walking behaviour and reason for stopping movement. The RM module had two submodels based on general assumptions of interactions among crabs (Null and FON). The two other modules had one submodel each. Additionally, IBU had a simple submodel describing the limited lifetime of unoccupied burrows.

Reason for movement

Random reason submodel (RM_r): This submodel followed the Null assumption of no interaction among the crabs, which therefore had a constant

probability P_{move} (Table 7.2) of leaving their burrow (if it was open) at each time steps.

Competition submodel (RM_{FON}): This submodel adapted the Field Of Neighborhood approach that was originally developed for trees and other sessile organisms (Berger and Hildenbrandt, 2000, 2003). The radius of interaction (R_{int}) was calculated for each crab at the start of the simulation with the following formula:

$$R_{int} = \min \{ a \times (CW/2) + b, R_{max} \} \quad (7.2)$$

where a and b were constants (Table 7.1), and R_{max} a maximum radius assumed to be 100 cm. R_{int} reflected the radius of daily action (excluding burrow change) of crabs according to their size and was estimated from field observations (Nordhaus, 2004; C. Piou, *personal observation*). The intensity of the FON at any point with distance r from a given crab was considered as (Berger and Hildenbrandt, 2000):

$$FON(r) = \left\{ \begin{array}{ll} 1 & \text{for } 0 \leq r < CW/2 \\ \exp\left(-\frac{|\ln(F_{min})|}{R_{int}-CW/2} \times \left(r - \frac{CW}{2}\right)\right) & \text{for } CW/2 \leq r \leq R_{int} \\ 0 & \text{for } r > R_{int} \end{array} \right\} \quad (7.3)$$

where F_{min} was the minimum intensity (0.01) of the FON at R_{int} . The sum of the FON intensity of the neighbors over the FON area of a given crab was then divided by its own FON area. The resulting value F_A is used as a measure of competition intensity. Note that this measure takes into account size (carapace width) and distance away from the neighbouring crabs. F_A was calculated at the beginning of each time step for each crab. When the crabs were individually checked, F_A was used to determine the probability of leaving (P_{move}) an already open burrow:

$$P_{move} = P_{base} \times \frac{F_A}{F_{A-max}} \quad (7.4)$$

where F_{A-max} was a constant to transform the competition intensity into probability of movement, and P_{base} was a base probability of changing of burrow at each time step (Table 7.2).

Walking behavior

The walking behavior was defined as the type and order of actions a crab would execute when it left its burrow and looked for another one or created a new one. This behavior was set as a repetition of three actions defining a movement step: 1) moving a short distance; 2) checking the surrounding

area; and 3) deciding whether to continue or not (described in the next module). The direction of movement was assumed to change between each movement step and was therefore calculated at the beginning of each step. A first random angle (α_0) was attributed to the crab at the beginning of its movement and the next ones (α_n) calculated as:

$$\alpha_n = \alpha_{n-1} + Rnd(\alpha_{dev}) \quad (7.5)$$

where α_{dev} was the “maximum deviation angle” and $Rnd(\alpha_{dev})$ an angle randomly taken from the interval $[-\alpha_{dev}, +\alpha_{dev}]$ (Table 7.2). The distance of a movement step was attributed randomly between 10 and 50 cm. On arriving at its new position the crab checked for all the burrows in a radius of perception, R_{move} , defined as:

$$R_{move} = C_{R_{move}} \times CW \quad (7.6)$$

where $C_{R_{move}}$ was a constant (Table 7.2). If no burrow was found in this area, the crab decided whether it should do another movement step or not (see next module). If burrows were found, the crab tried to take them over. This takeover was impossible if a burrow was occupied, and followed different probabilities of success in the other cases (parameters P_{c1} to P_{c3} , Table 7.1). The crab kept in memory the burrows that it had visited since the beginning of the walk. If an occupied burrow had been previously checked, the probability of success of taking over was set to zero.

Reason for stopping movement

The first reason for stopping was whether it managed to take over another burrow. The crab position was then set to this burrow position. If no burrows were taken over at this step, the crab continued moving with probability $1 - P_{stop}$ (Table 7.2), or else created a new burrow at its actual position.

Burrow lifetime submodel

Empty burrows sooner or later disappear from mangrove floor because of tidal wash and bio-perturbation. To model this in a simple way, the probability of disappearance (P_{disap}) of the empty burrows, was determined as:

$$P_{disap} = c_{disap} \times t_{empty} \quad (7.7)$$

where c_{disap} was a constant defined as the “disappearing factor of burrows” (Table 7.2) and t_{empty} the number of days since a crab last occupied the focus burrow. Thus, the longer a burrow was without a crab, the higher the probability of its disappearing, until the burrow would disappear deterministically after the time $t_{empty} = 1/c_{disap}$.

Table 7.2: Descriptions and values of parameters tested with the two models, analyzing their effect on empirical pattern reproduction.

Parameter name	Description	Values tested with the Null model	Values tested with the FON model
P_{move}	Probability of movement at each time step	0.01, 0.1, 0.2, 0.3	-
P_{base}	Base probability of movement at each time step (Eq. 7.4)	-	0.1, 0.2, 0.3
P_{stop}	Probability of stopping movement at each movement step	0.001, 0.002, 0.004, 0.008	0.002, 0.004, 0.008
$c_{R_{move}}$	Constant for the radius calculation of crabs perception of burrows at end of movement-steps (Eq. 7.6)	1, 2, 3, 4	1
α_{dev}	Maximum deviation angle between each movement step (Eq. 7.5)	$\pi, \pi/2, \pi/4, \pi/20$	$\pi/4$
c_{disap}	Disappearing factor of burrows (Eq. 7.7)	0.15, 0.07, 0.02, 0.005	0.02
F_{A-MAX}	Maximum FON neighbors effect a crab could feel without increasing its probability to leave its burrow (Eq. 7.4)	-	0.1 to 1.9 with increment of 0.2

7.4.2 Model analysis

Two different models were analyzed to find the parameterization that best fit the patterns observed in the field experiments. The first model used only the Null assumption of interaction between crabs (RM_r) (hereafter referred to as Null model). Five parameters that were hard to estimate from field knowledge were considered to have a possible influence on the re-colonization patterns (Table 7.2). Four values were assigned for each of these parameters and all possible combinations of parameter values were tested. For each parameter set, two types of simulation experiments were performed, which correspond to the field experiments 1 and 2: removing of all burrows and crabs

of a $12.25 m^2$ area (experiment 1), and removing only the crabs of an identical area but leaving the burrows (experiment 2). The simulations lasted 50 or 15 days respectively after the initial phase of randomization/organisation of 10 days. Note, that both experiments mimic the field experiments carried out during this study. They do not imitate the traditional behaviour of crab collectors, who catch only big males and do not concentrate on a quadrature area. Thirty replicate simulations of each type of experiment were performed. To check the fit to the two linear patterns of re-colonization observed in the field (Fig. 7.1), an error of deviation from each pattern (ΔRec) was calculated with the formula of root mean square deviation (e.g. Jamieson et al., 1998; Wiegand et al., 1998):

$$\Delta Rec = \sqrt{\frac{\sum_{t=1}^{N_{obs}} (F(t) - Sim(t))^2}{N_{obs}}} \quad (7.8)$$

where N_{obs} was the number of days of observations (50 for the first experiment and 15 for the second), $F(t)$ was the regression describing the observed linear recovery of the percent of occupied burrows at time t after fishery and $Sim(t)$ was the corresponding simulated value. A total error estimation (ΔTot) was calculated as:

$$\Delta Tot = \sqrt{\Delta Rec_{exp1}^2 + \Delta Rec_{exp2}^2} \quad (7.9)$$

where ΔRec_{exp1} and ΔRec_{exp2} are the error of deviation for experiment 1 and 2, respectively (from Eq. 7.8). Additionally, the proportion of crabs that moved per time step and the proportion of occupied burrows on the entire area were registered and compared to field estimations. To understand the relative effects of parameters and their interaction on the total error (deviation between simulated and regressed dynamics of re-colonization), a general linear model (GLM) was computed as a large design ANOVA. Multiple comparisons among means of groups were based on Tukey's "Honestly Significantly Different" tests in order to differentiate homogeneous groups of parameterizations that could be considered as having identical fit to the field patterns.

The second model included local competition among crabs using the FON approach in the reason for moving submodel (RM_{FON}) (hereafter referred to as FON model). Three base probabilities of movement (P_{base}) and probabilities of stopping movement were tested, respectively (Table 7.2). For the parameter F_{A-max} of calibration of the FON intensity, ten values were tested (Table 7.2). With these 30 possibilities for P_{base} and F_{A-max} combinations, we covered a large range of P_{base}/F_{A-max} ratios as an index of transformation of FON intensity (F_A) into probability of leaving (Eq. 7.4, P_{move}). For each

of the parameters c_{Rmove} , α_{dev} and c_{disap} a value was chosen based on the results from Null model (Table 7.2; a similar approach for parameterization is used by Mullon et al., 2003). Thirty replicates of each possible parameter's configuration were performed for both fishery experiments, 1 and 2. The deviations from the field patterns were calculated with the same estimations of error described above (ΔRec_{exp1} and ΔRec_{exp2} Eq. 7.8, and ΔTot Eq. 7.9). To be able to compare the two model versions (Null and FON), the results of the Null model with identical parameter set ($c_{Rmove} = 1$, $\alpha_{dev} = \text{Pi}/4$, $c_{disap} = 0.02$) were considered. The mean frequency of movement of crabs were measured during the simulations.

7.5 Results

7.5.1 Null model

All tested parameters significantly influenced the total error of recovery pattern (GLM with all parameters as grouping variables and all cross interactions, all $p < 0.05$, Adjusted $R^2 = 0.836$). Smaller “maximum deviation angle” between movement steps reduced the total error (Fig. 7.3) by decreasing the erratic type of movement. Likewise, a smaller radius of the crab's perception of burrows also decreased the total error (Fig. 7.3) by increasing the probability of finally creating a new burrow, and therefore increasing the probability of colonizing the fished area. The longer the lifetime of empty burrows (low c_{disap}), the better the simulations were at fitting the recovery patterns. This was particularly true for experiment 2, which could better reproduce the high recovery proportion at the beginning of recolonization with long-lasting burrows.

The probability of movement was seen as one of the most important parameter influencing the recovery patterns with higher frequency of movement leading to better fits (Fig. 7.4). However, the total error of simulations with $P_{move} = 0.3$ were not significantly lower than with $P_{move} = 0.2$ because with a too-high frequency of movement, simulations led to a very high recovery rate for experiment 1. The probability of stopping movement together with the maximum angle of deviation determined the distance walked by crabs. This altered the recovery pattern fit in cases of extremely short or extremely long walks. Too short or too long walks led to no movement crossing the fished areas or higher probability of finding an empty burrow somewhere else in case of experiment 1, therefore leading to slower recovery. The 81 best fitting parameterizations (lowest ΔTot) were not found to be significantly different (Tukey HSD test; Homogeneous groups, Between MS = 0.00343, df = 29696).

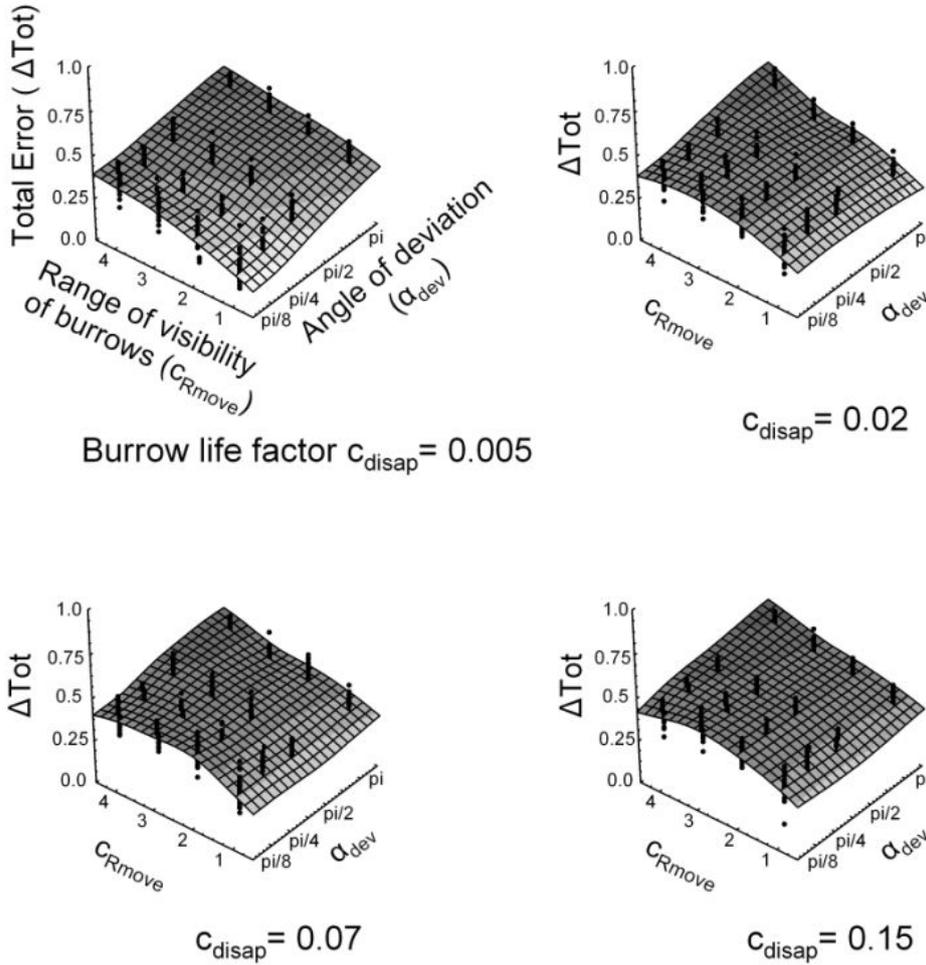


Figure 7.3: Effects of maximum deviation angle during movement (α_{dev}), range of crab's perception of burrows (c_{Rmove}) and disappearing factor of burrows (c_{disap}) on the reproduction of the recovery patterns (Total Error ΔTot). Data selected for this graph had all identical probability of movement ($P_{move}=0.1$) and probability of stopping ($P_{stop}=0.004$). Each point corresponds to one simulation result.

They were mainly following the previously described trends: including high probability of movement, intermediate walking distance, small radius of burrow perception and long lifetime of empty burrows on the surface.

However, these parameterizations required probabilities of movement which led to high measured frequencies of movement to obtain the best fits. These frequencies of movement were much higher than the estimate of 15% of crabs per day leaving their burrows.

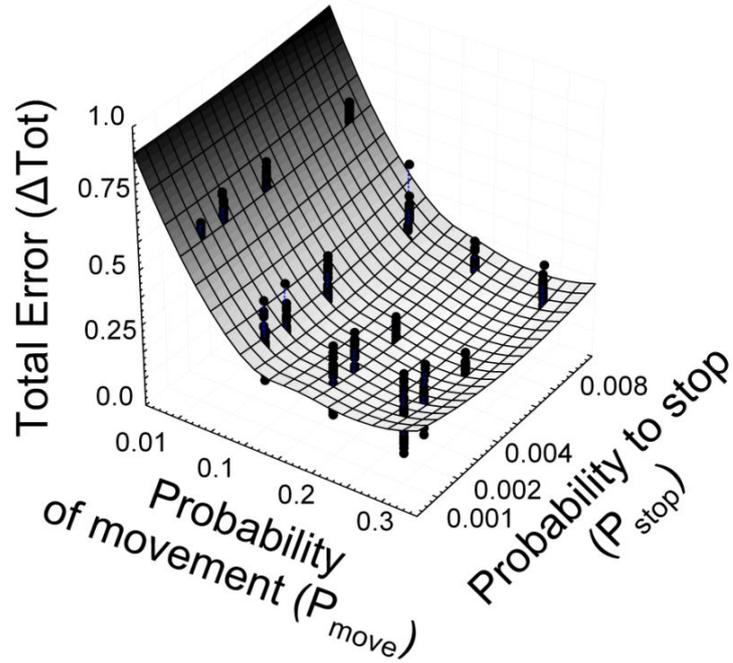


Figure 7.4: Effects of probability of movement (P_{move}) and probability to stop moving (P_{stop}) on the reproduction of the recovery patterns (Total Error ΔTot). Data selected for this graph had all identical maximum deviation angle ($\alpha_{dev} = \pi/4$), disappearing factor of burrows ($c_{disap} = 0.02$) and range of crab's perception of burrows ($c_{Rmove} = 1$). Each point corresponds to one simulation result.

7.5.2 FON model

With the use of the FON submodel (RM_{FON}), the ratio of P_{base}/F_{A-max} determined the overall error (ΔTot) and the measured frequency of movement of crabs during the simulations (Fig. 7.5). At intermediate P_{base}/F_{A-max} ratio (~ 0.003 to 0.007), the mean total error showed best fits to the field pattern of recovery (Fig. 7.5), indicating an optimal range of frequency of movement with the FON model. The probability of stopping movement also had an effect on these total errors, showing better fits with higher P_{stop} values (Fig. 7.5). But for the three P_{stop} values tested, similar patterns of effect of the P_{base}/F_{A-max} ratios on the total error were observed (Fig. 7.5). Among these parameterizations, the variance of total error was not identical, and assuming that a better parameterization would be the one reproducing the field pattern more often, the best parameterizations were believed to be the ones with smaller variance of total error.

Figure 7.6 shows the mean total error of each parameterization using the FON model against their respective variance. Additionally the selected

Mean Total Error

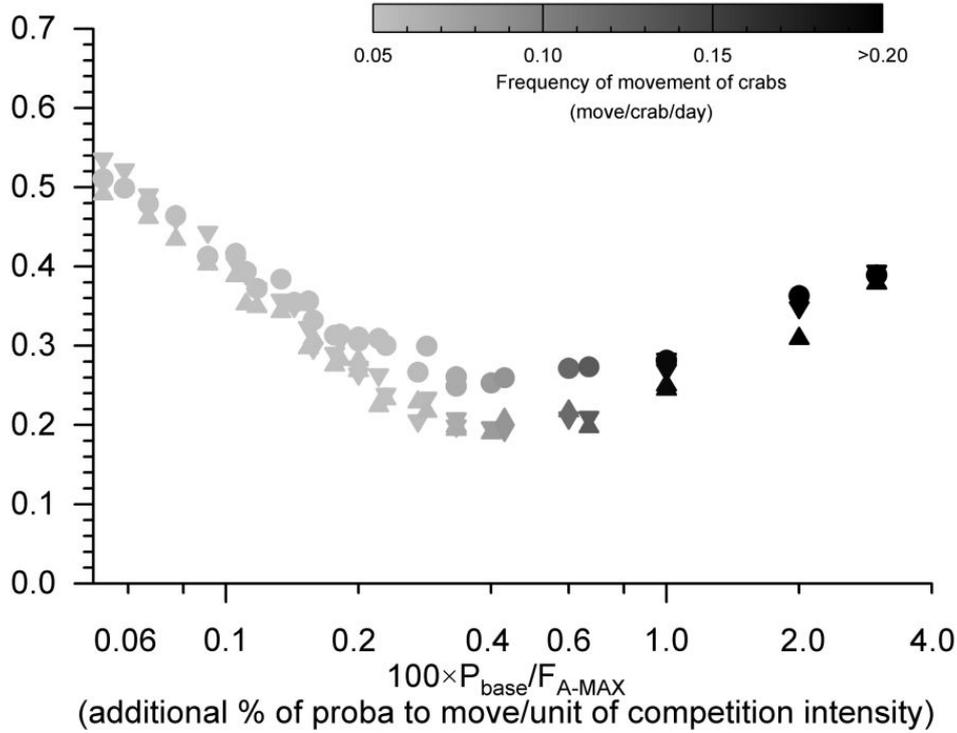


Figure 7.5: Effect of the scaling parameter to transform competition intensity to additional probability of movement ($100 \times P_{base}/F_{A-MAX}$, axis= $\log(x)$) on the mean total error of deviation from the field pattern of recovery with the second type of models. Circles: $P_{stop} = 0.002$; Upward triangles: $P_{stop} = 0.004$; Downward triangles: $P_{stop} = 0.008$. Gray intensity of markers represents the mean frequency of movement of crabs during simulations. Each point represent the mean of 30 replicates, variations of means were not presented here to facilitate reading (see Fig 7.6 and 7.7).

corresponding parameterizations of the model using the Null interaction sub-model were also plotted on Fig. 7.6. For this Null model, the parameterization leading to the lowest mean total error was not realistic in terms of measured frequency of movement (>0.20 move/crab/day, parameterization α_1 on Fig. 6b: $P_{move}=0.3$, $P_{stop}=0.004$). Considering a more realistic frequency of movement, the most realistic parameterization could be selected (β_1 on Fig. 7.6: $P_{move}=0.2$, $P_{stop}=0.004$) for this Null model. For the FON model, high frequency of movement led to high mean total error and high variance in the fit of the field patterns. Some parameterizations leading to very low mean total error were also observed with relatively high variance (e.g. the smallest mean total error given by parameterization α_2 on Fig. 7.6b: $P_{base}=0.3$, $P_{stop}=0.008$ and $F_{A-max}=0.7$). We could select the best and most

realistic parameterization considering a compromise between the goodness of fit, the low variance and the low frequency of movement (β_2 on Fig. 7.6b: $P_{base}=0.3$, $P_{stop}=0.008$ and $F_{A-max}=0.9$).

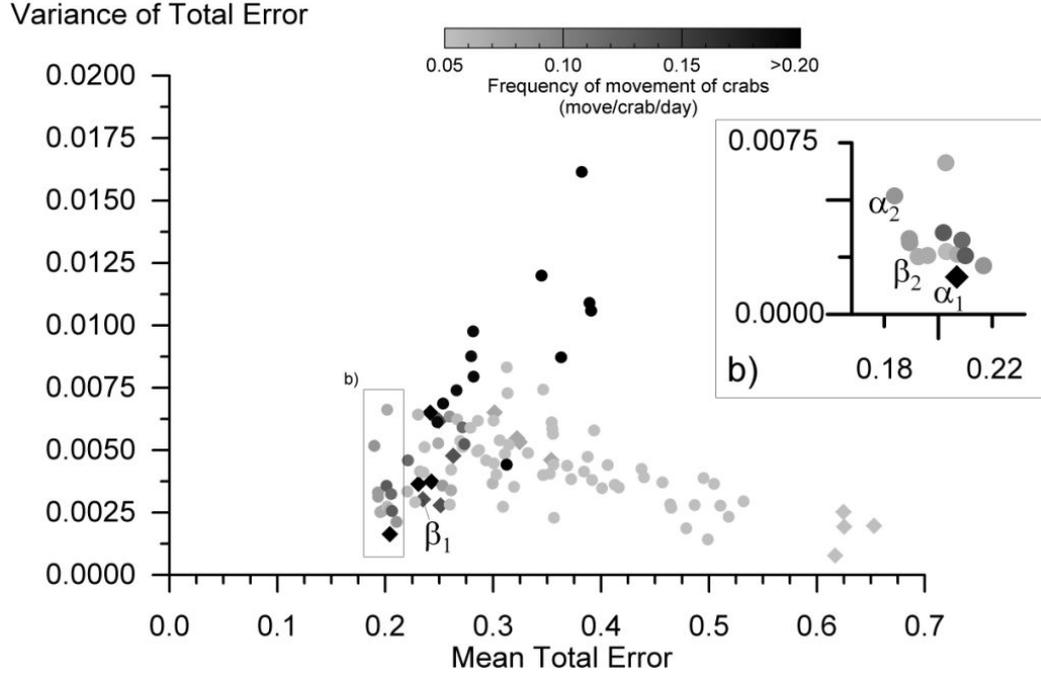


Figure 7.6: Mean total error against variance of total error in the reproduction of the recovery pattern for the parameterizations of the second model type (using the RM_{FON} submodel, circles markers) and selected parameterization of movement step behavior ($c_{R_{move}}=1$, $\alpha_{dev}=\pi/4$, $c_{disap}=0.02$) of the first model type (using the RM_r submodel, diamonds markers). Parameterizations on the lower left corner are the best and more reliable parameterizations (zoomed in on part b). Gray intensity of markers represent the mean frequency of movement of crabs during simulations (black markers are not realistic with a frequency higher than 0.20 move/crab/day, i.e. >20% of the population move every day). Greek letters refers to best parameterizations following only the mean total error (α_1 and α_2 of respective model types) and selected best parameterizations according to a compromise between the mean total error, the variance and the frequency of movement (β_1 and β_2 of respective model types).

The FON model in general needed lower mean frequency of movement of individual crabs to achieve better range of goodness of fit than the corresponding Null models (Fig. 7.6). This was also true for the two selected most realistic parameterizations of the respective two types of models (β_2 with 0.065 moves/crab/day had lower mean total error than β_1 with 0.137 moves/crab/day). These two selected most realistic parameterizations were distinct in their fit to the field patterns mainly because β_2 reproduced better

the linear recolonization in experiment 1 and had a faster recovery in experiment 2 than with β_1 (Fig. 7.7). The reason for movement according to the intensity of competition (RM_{FON}) allowed therefore to have better fits and more realistic frequency of movement than assuming only a random reason for the crabs to change burrows (RM_r).

7.6 Discussion

Overall, our field experiments confirmed the statement of *U. cordatus* collectors that fished areas are recovered within two weeks. However, in our field experiments, we achieved a maximum recovery rate of about 80% during this time frame, which also confirms the results of Diele (2000). Several factors explain the small discrepancy between the statement of the crab collectors and the results of our experiments: crab collectors collect only large males while we removed crabs of all sizes during our field experiments. Furthermore, crab collectors do not concentrate on a small area as we did, but walk around in the forest catching a crab here and there without probing every large burrow and thus never entirely depleting all large males along their path. Finally, their perception of recovery is not quantitative and what they call full recovery might not be 100%.

Nevertheless, the linear recovery phenomena are important population-level patterns since they demonstrate that *U. cordatus* indeed regularly moves from one burrow to another despite the fact that we found rather little evidence of this from direct behavioural observations in the field. This cryptic movement behaviour resulted in a high uncertainty of data regarding the frequency of crabs' movement. The maximum estimate of 15% of the crabs moving per day was considered as an extreme value because it would imply that crabs change their burrows every ~ 7 days on an average. Such a high turn-over of burrows does not seem compatible with the field observation that *U. cordatus* spends $> 90\%$ of its time inside or inactive on top of its burrows (Nordhaus, 2004).

The field experiments further revealed that a fished area recovers much faster when holes are left on the sediment after the passage of the crab collector. *Ucides cordatus* obviously prefers to establish itself in an already created hole than to dig an entirely new one. This observation indicates that burrows are precious resources, energy-expensive to build and conserve. Thus, the question as to which factor forced a crab to change its burrow instead of staying where it was before arose. According to Nordhaus et al. (2006), the Caeté crab population is food limited, indicating competition among neighbouring crabs. Based on the information on individual behaviour and on

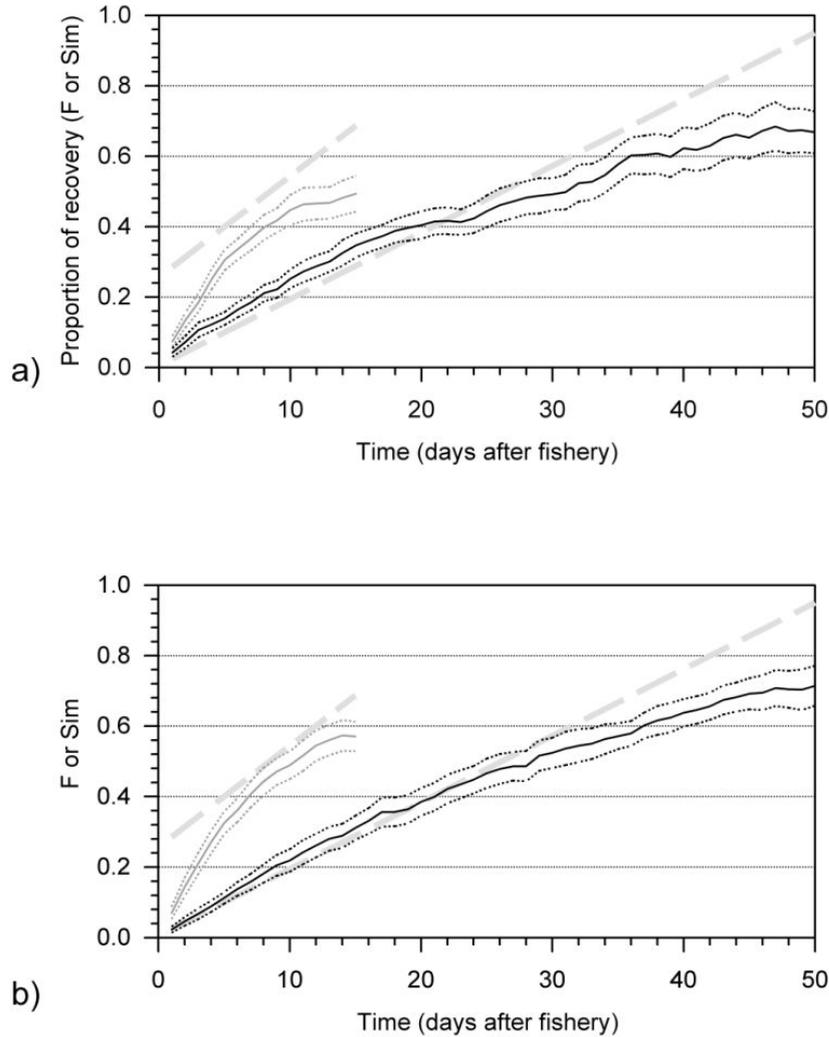


Figure 7.7: Recovery patterns of the most realistic and best fitting parameterizations for the two type of models: a) using the no-interaction submodel (RM_r) (parameterization β_1 : $P_{base}=0.2$, $P_{stop}=0.004$, $c_{Rmove}=1$, $\alpha_{dev}=\text{Pi}/4$, $c_{disap}=0.02$); b) using the FON submodel of interaction (RM_{FON}) (parameterization β_2 : $P_{base}=0.3$, $P_{stop}=0.008$, $F_{A-MAX}=0.9$) (Solid black and grey lines: mean of proportion of recovery after fishing from 30 simulations experiment, with removing the burrows or leaving the burrows respectively; black and grey dashed lines: corresponding confidence interval; interrupted bold light grey lines: field patterns of recovery, c.f. Fig 7.1).

recovery pattern on the plot level, simulation experiments were considered as most suitable to test whether crab movement triggered by local competition could explain the linear recovery patterns observed in the field.

By definition, local or neighbour competition occurs among individuals

that interact with each other. Thus, we considered an individual-based, spatially explicit model as an adequate tool. Existing individual-based models implying competition among moving animals either explicitly describe resources use (e.g. Cuddington and Yozdis, 2000; Railsback and Harvey, 2002) or indirectly represent competition by assuming movement to be density-dependent (e.g. Taylor, 1981; Mogilner et al., 2003). Both of these approaches have their pros and cons: the direct approach is mechanistic, but requires detailed knowledge on behaviour and resource dynamics. The indirect approach does not represent feeding behaviour but the direct interactions among individuals (by proximity, fight or territoriality). It transforms distances of individuals into forces and direction of movement of the individuals for the analysis of animal aggregations (e.g. Mogilner et al., 2003). Thus, this second type of approach assumes interference competition (animals interact directly) and not exploitation competition (competition through the use of identical resources without direct interactions, definitions following Keddy, 1998). We needed both in our case.

For these reasons, we chose an approach that is in between the direct and indirect approaches to modelling movement: interactions among crabs are modelled explicitly but without directly referring to feeding, resources or agonistic interactions. This kind of modelling of local interactions has a long tradition in plant ecology (Czárán, 1998) but there is no reason why it should not be used for animal ecology as well. To our knowledge, there is only one previous attempt to model interactions among animals and among animals and plants in a similar way: the GECKO model (Booth, 1997) which is applied in microbial ecology (Kreft et al., 1999; 2001) and for arthropod food webs (Schmitz, 2001). In GECKO, individuals are assumed to have a circular zone-of-influence and zone overlaps are considered as interaction. Individuals are represented by spheres rather than the more dome-shaped field-of-neighbourhood, and the details of how interactions are implemented are different. Moreover, the mode of interaction of GECKO has never been analysed by itself or contrasted to other modes, including a Null model of no interaction at all. In contrast, the properties of the FON approach have been analysed in great detail (Bauer et al., 2002; 2004; Berger et al., 2002; 2004; Berger and Hildenbrandt, 2003).

Nevertheless, the applications of GECKO confirm our conclusion from using the FON approach for modelling local interactions among animals: the approach is conceptually simple and constitutes a good compromise between too-detailed and too-highly aggregated approaches. Berger et al. (2002) argue that the FON approach, or similar approaches, could be developed into a standard way of representing local interactions among plants. Here we would like to conclude that FON and similar approaches, which are based

on the notion of a zone of influence, could and should also be developed into a standard approach for representing interactions among animals. Such standard building blocks are needed for developing individual-based models of communities and ecosystems (Grimm and Railsback, 2005).

We show that, at least if resources are distributed and replenished homogeneously, the FON approach is well suited for describing the competition intensity that each crab exerts on this resource. Since Nordhaus (2004) observed that *U. cordatus* generally stays close to its burrow and has a higher chance of obtaining leaves that land on the ground close to its burrow entrance, we considered that the highest competition intensity a crab exerts is at its burrow position, and this intensity should decrease with increasing distance from the burrow. The FON approach with an exponentially decreasing field was then believed to simulate the competition interaction among individual crabs well. A comparison with other approaches coming from plant interaction models such as Fixed Radius Neighbourhood and Zone Of Influence (ZOI) (e.g. Czárán, 1998, chapter 6.3, p218) could inform about the specific type of intra-specific competition but this could not be done within the scope of this study.

We also did not address differences between rooted and non-rooted areas. As mentioned above, crab collectors cannot fish underneath dense *R. mangle* roots. These areas are, therefore, considered as buffers against rapid over-fishing as they are likely to promote the recovery of fished areas. However, we do not yet have any information upon how the crabs' behaviour differs among habitat types. Thus, in the model we assumed the area surrounding the fished plot to be homogeneous. Since our experiments produced different crab densities, i.e. within and outside the fished area, we indirectly tested the relative importance of neighbour competition depending on habitat quality but not the impact of habitat heterogeneity.

The Null version of the IBU model was used as an *a-priori* test of the importance and range of movement parameters. Comparing simulation results with field data, a medium rate of burrow disappearance and an intermediary "maximum deviation angle" were selected as the most reliable parameters. In combination with an individual's probability to stop and the radius of a crab's burrow perception, these parameters were linked to the distance covered by the crabs and the probability that a crab settles inside a fished area. Not surprisingly, the probability of crab movement was the most important parameter affecting the recovery of fished areas for that model version. Highest movement frequencies fitted the linear recovery patterns observed in the field best. These frequencies exceeded, however, the maximum value observed in the field. The Null model version thus revealed that non-triggered movement can not explain the observed linear recovery in the field because

it requires unrealistically high movement frequencies.

In the second version of the IBU model, the frequency of movement is linked to the competition among crabs, and expressed by the overlap of their Field-of-Neighbourhoods (FONs). This description assumes an impact of food competition, suggested by Nordhaus et al. (2006) on the frequency of burrow change of *U. cordatus* in the study area. It resulted in a significant decrease of the movement frequency necessary to reproduce the linear recovery pattern. Crabs under high competition in the non-fished areas move more frequently than specimens under low competition, such as those already re-established in the fished area. These results imply that movement is triggered by competition for resources, and is therefore density-dependent. Perturbation of burrow entrances might also trigger crab movements (C. Piou, *personal observations*). This factor should be investigated systematically in the field. However, such perturbations are likely to be random events and are thus indirectly considered by our Null model.

Density-dependent movement is a characteristic behaviour that has implications for the management of *U. cordatus* as a resource for human populations. In areas of *R. mangle* dominated forests that are easy to access, large males are frequently fished. The crabs hidden under the roots are not accessible to the crab collectors and probably replace the fished ones because of higher density (Piou et al. *unpublished data*) and therefore higher competition under the roots than on the accessible areas. Additionally, we observed with the different parameterizations of the IBU model that *U. cordatus* shall not walk too long distances for the linear recovery pattern to be reproduced. Thus, comparing the local non-fished areas of high root density to the peninsula level less-fished areas, the former are probably more important as a local buffer system for the recovery of artisanally fished areas. This argues in favour of keeping the traditional catching methods and not harvesting these local buffers by more advanced techniques as observed in other places of Brazil (*Personal communications*). The peninsula level less-fished areas such as *Avicennia germinans* dominated forests, or eventually the less-visited *R. mangle* forests, might not act as buffer within an identical time frame because they are further away. However, as long as intraspecific competition of *U. cordatus* is high in these areas, they could function as large scale buffer system refilling the local scale buffers. The impact of fishing techniques allowing crab collectors to fish in these areas should be analyzed to conclude on their possible need of regulation. However, the capacity of both the local and the peninsula level buffer systems would depend ultimately on recruitment as under a hierarchical system. The relative importance of these buffer systems versus the recruitment processes is still to be investigated.

In the case of the Caeté peninsula which was not intensively exploited

until the end of the 80's (Diele et al., 2005), overall change of buffer capacity because of harvesting within all mangrove areas might explain the 6 and 8% drop in catch per unit effort in the late 90's. If the hierarchy of buffer systems hypothesized above is correct, this would then suggest that the competition-induced local recovery rate that we observe today could have been much faster several decades ago when fishery was less intensive. This coincides with crab collectors' statements (Senhor Manuel and Domingos de Arajo, *personal communications* to C. Piou) that fishery of large males could be done much faster several decades ago. Further study could investigate these aspects at multiple scales. Our IBU model could be used in the future to quantify the buffer capacity at local scale and to explore how it is indirectly related to recruitment. Larger-scale analysis might then inform how the buffer systems and the overall recruitment affect the rate of recovery and thereby help establish the sustainable yield that can be taken from the system.

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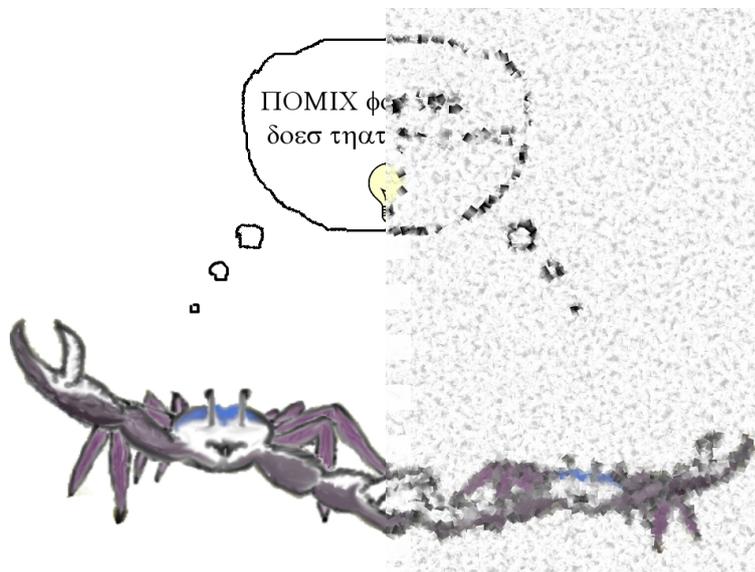
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Chapter 8

Testing intraspecific
phenomenological competition
models at individual-level to
reproduce population-level
patterns of a mangrove crab



Testing intraspecific phenomenological competition models at individual-level to reproduce population-level patterns of a mangrove crab

Cyril Piou¹

Article in preparation

8.1 Abstract

Intraspecific competition among individuals of the semi-terrestrial crab *Ucides cordatus* was demonstrated to happen in a north-Brazilian mangrove forest. Previous studies also hypothesised that competition was the main factor driving population spatial organization and individual movements of change of burrows. However, the link between individual behaviour and competition was so far not entirely analyzed. The main objective of the present study was to assess different types of behavior represented by different individual-based models for their capacity in reproducing population level patterns. The Individual-Based *Ucides cordatus* (IBU) model was adapted to use different phenomenological competition models corresponding to symmetric or asymmetric competition behavior and different size of harvesting area. The pattern-oriented modeling information criterion and mean squared deviation were used to assess the goodness of fit of these models to patterns of recovery after fishery and spatial organization on a small scale (<10m). The results confirmed the role of competition as a main factor driving spatial organization but were less categorical for the recovery patterns. The overall best fits were obtained with models implying a higher importance for close-by resources than further away ones. Further study on frequency of movements related to the size of the crabs could inform on the role of asymmetric competition among individuals of different sizes hypothesized to happen with the best fitting model of the present study.

Key Words: *Ucides cordatus*, phenomenological individual-based model, pattern-oriented modeling, intraspecific competition, asym-

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metric/symmetric competition**8.2 Introduction**

The semi-terrestrial crab *Ucides cordatus cordatus* (L. 1763) (hereafter referred to as *Ucides cordatus*) is an important ecological component (Branco 1993, Blankenstejn et al. 1997, Wolff et al. 2000, Koch and Wolff 2002, Schories et al. 2003, Nordhaus et al. 2006) and economic resource of Brazilian mangrove forests (Glaser 2003). In the frame of the MADAM project (Berger et al. 1999), *U. cordatus* was the subject of different study on its biology (Diele 2000, Nordhaus 2004, Nordhaus et al. 2006, Diele and Simith. 2006, Chapter 7) and population structure (Diele 2000, Diele et al. 2005, Chapter 6). The feeding behavior of *U. cordatus* was particularly well documented with the work of Nordhaus (2004) who showed that the preferred food of this crab are leaves falling from *Rhizophora mangle* trees. She also demonstrated from these feeding studies that *U. cordatus* was food limited and thus intraspecific competition among individuals might occur. Intraspecific competition was demonstrated to explain crab movements of change of burrows explaining the recovery of fished areas (Chapter 7) and proposed as a main factor organizing spatially the crab population (Diele 2000, Chapter 6). The observations of Nordhaus (2004) on individual behavior showed that *U. cordatus*, as many other Brachyuran crabs, have territorial behaviors and particularly in relation to the use and protection of their burrows. These observations hypothesized that both interference competition (animals interact directly to obtain a resource) and exploitation competition (competition through the use of the resource without direct interaction, definitions following Keddy 1989) could happened among individuals. Nordhaus (2004) described that both the fights and harvesting are usually occurring within a small area around their burrows. However, the actual knowledge can not tell the distance until which the sense of these two mechanisms of competition would eventually lead a crab to go away from a highly demanded area.

The work of Nordhaus (2004) also demonstrated a non-linear relationship among gastrointestinal content and size of the crab, showing a tendency for small crabs to need, proportionally to their weight, more resources than bigger crabs. She observed also that the bigger crabs assimilate slower their food than smaller crabs. These findings would suggest that the impact of loosing some available food because of the presence of other crabs have a non-proportionally higher impact on starvation of small crabs than on bigger ones. In the competition for food context, this could be interpreted as an asymmetric competition situation. Moreover, Nordhaus (2004) behavioral

observations showed that in fights situation, the larger individuals win most of the time. Thus, asymmetric competition is occurring in interference competition among individuals as well. Competition can always show different degree of symmetry/asymmetry (Schwinning and Weiner 1998), but fundamentally asymmetric competition would mean a disproportionate advantage for larger individuals (relative to their size) over smaller ones. Asymmetric competition in plant populations might sometimes be a reason for a wider size distribution than expected (Schwinning and Weiner 1998). Chapter 6 proposed that the spatial organization of *U. cordatus* at the peninsula level, finding large individuals in most favorable habitats and small ones in secondary habitats, could be a result of asymmetric competition.

Ucides cordatus populations are therefore showing interference and exploitation intraspecific competition with possible tendency for asymmetry. However, there is no information so far on the relative implications of all these different aspects of intraspecific competition in the decision of crabs to change burrows. Identically, the specific aspects of competition that could lead to the regular spatial organization of individuals at small scale (<10m) seen in Chapter 6 are not known. Particularly, understanding the role of asymmetric competition at the individual level could help in explaining the patterns of population organization at the peninsula level as proposed in Chapter 6. Thus, a series of questions are still to be investigated on these aspects. The present study will focus on the following two: - does the supposed asymmetric competition occurring among individuals plays a game in the recovery of the crab population after fishery and the spatial organization ? - and does the territorial behavior and the indirect competition for food show a trend of spatial importance such that food and/or territory (altogether from now-on considered as “resources”) closer to the burrow are more important than further away ?

Chapter 7 proposed to analyze the type of interactions among individuals with different individual-based competition models. Secondary observations of individual-based models developed in a pattern-oriented modeling framework can lead to findings as interesting as the explanation of the original focus patterns (Wiegand et al. 2003, Grimm et al. 2005). The available individual-based model simulating *U. cordatus* individuals (IBU) was developed with a pattern-oriented modeling approach and tested to reproduce patterns at population level. IBU simulates competition with a phenomenological approach, i.e. not all the steps of resource use are simulated mechanistically. This approach was the field of neighborhood (FON) developed by Berger and Hildenbrandt (2000) which is a particularly good example of phenomenological model simplifying competition among individuals but still reproducing many processes and associated patterns (e.g. Berger and Hildenbrandt 2003,

Berger et al. 2002, 2004, 2006, Bauer et al. 2002, 2004). In IBU, the mathematical structure of FON assumes that for a crab to decide to change of burrow, the resources further away are less important than the one close to the actual burrow. Also, according to Bauer et al. (2004), the FON approach simulates asymmetric competition. Thus this approach had already assumptions about the two focus questions of the present study. Other individual-based approach might however be considered to test these assumptions. For example, another one known to simulate asymmetric competition (Weiner et al. 2001) is the zone of influence approach (ZOI). The fixed radius neighborhood (FRN) approach is a simpler phenomenological way of describing competition among individuals (Pacala and Silander 1985). This approach considers the *competition intensity* (i.e. the pressure of all the neighbors on the common resource of an individual, Keddy 1989) to be directly linked to the density of neighboring individuals on a harvest or resource use area, and thereby does not give more weight to close-by resources. The differences of mathematical structure and possible derived assumption of behavioral representation of these three types of individual-based approaches simulating competition (FRN, ZOI and FON) give already a panel of possibilities in term of competition symmetry and proximity of resources. Changing the size of the radius of interaction which is the base of these three models would also allow assessing further the question of importance of the proximity of resources.

The present study consider consequently these three different phenomenological ways of simulating competition at the individual level with different size of radius of interaction. The main purposes were to investigate: (1) if the behavior of *U. cordatus* showed different resource importance depending on the distance to the burrow, and (2) if the crab use of resources led to an asymmetric competition condition. To infer on these questions, I analyzed under which assumptions of IBU three population-level patterns were reproduced. In addition to the two recovery patterns after local fishery, as analyzed in Chapter 7, I tried here to reproduce also the spatial organization at small scale (<10m) documented in Chapter 6. Thereby, I aimed in verifying the assumptions of Chapter 6 that competition among individuals is a probable factor leading to spatial organization of their burrows because of their movement.

8.3 Methods

8.3.1 The IBU model

The IBU model was developed to simulate individual *U. cordatus* behavior at small scale, primarily to understand the phenomenon leading to recovery of fished areas (Chapter 7). The IBU model is a self-standing object-oriented program developed in C++ (Stroustrup, 1997) and was extensively described in Chapter 7 using the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006). In the present chapter, I indicate just the changes operated to the original version.

The sub-models of reason for crab movement were the focus of the present study. I considered 3 sub-models of competition at the individual level (2 more than in Chapter 7) assuming that competition is the factor triggering the crabs to change burrow and one null sub-model describing the change of burrow as a random event (described also in Chapter 7). Each sub-model determined the probability that a crab has to move away from its burrow to find or create a new burrow in another location. This could be called the *competition effect*. To use phenomenological approaches thoroughly, the simplified phenomena need to be clearly defined as well as the limits and assumptions. Thus, to adapt the three different phenomenological approaches to the IBU model, they should handle competition in a comparable way. I assume that all three sub-models should lead to the estimation of a *competition intensity* felt by each individual. I define for this purpose the term *competition intensity* as a phenomenological evaluation of the pressure of competing organisms on the resources wanted by a focus organism. This *competition intensity* should be then transformed into a *competition effect* in identical way. The 3 sub-models of competition were based on estimating the *competition intensity* felt by a focus crab in an interaction area. They used an identical calculation of the interaction area, defined as a circular zone of interaction around the burrow of a crab. The radius of interaction (R_{int}) was calculated for each crab at the starting of the simulation with the following formula:

$$R_{int} = \min \{ a \times (CW/2) + b, R_{max} \} \quad (8.1)$$

where CW was the crab carapace size (in cm), a and b were constants (values of $a= 5, 10$ or 19 , cf. below, values of $b=15$), and R_{max} a maximum radius assumed to be 100 cm (Nordhaus 2004). The surface of the area of interaction A_{int} was therefore:

$$A_{int} = \pi \times R_{int}^2 \quad (8.2)$$

In the first IBU version (Chapter 7), R_{int} reflected the radius of daily action

(excluding burrow change). The size of the daily action radius was assumed to be related to crab size. However, competition might be influencing crab decision to change burrow only on a shorter zone, i.e. the importance of resources away from the crab might not be leading to decision to change burrow if the closer resources are not shared with other crabs. Thus, I tested 3 values of the parameter a to analyze if the interaction area leading to crab movement was corresponding to the entire harvesting area or not. I now describe the 4 sub-models of reason of movement tested in this exercise.

Sub-models of reason for movement

Random reason submodel (RM_r): This sub-model followed a null assumption of interaction: crabs do not move because of spatial competition for food. Crabs had therefore a constant probability P_{move} of leaving their burrow (if it was open) at each time steps.

Density related competition sub-model (RM_{DENS}): This sub-model was inspired after the fix radius neighborhood approach (Pacala and Silander 1985), except that in this approach the radius of interaction was not fixed but size dependent (cf. Eq. 8.1). The number of crabs within the interaction area was counted at each time step (N). N was used to determine the *competition effect*, i.e. the probability of leaving (P_{move}) an already open burrow, according to the following formula:

$$P_{move} = \frac{C_N \times N}{A_{int}} \quad (8.3)$$

where C_N was a scaling constant to obtain a wanted mean frequency of movement of the population (further explanations in “parameterization” part below, and see Table 8.1 for values). I assumed with this equation that the *competition intensity* (i.e. the pressure on the common resource) on an individual was related to the density of competing neighbor (N/A_{int}). Since the *competition intensity* was not dependent on the actual need of resources of the neighbors, this sub-model could correspond to a territorial behavior of individuals in competing either directly or indirectly to assure their resource needs.

Homogeneous intensity competition sub-model (RM_{ZOI}): This sub-model was adapted after the zone of influence models (ZOI, as described in Czárán 1998, pp219, 231-239). The ZOI of an individual represents the spatial resource in use. I did not share mechanistically with rules the resource among crabs with overlapping ZOI, as it is done in most ZOI models (e.g. Bonan 1991). I assumed that the proportion of overlap of interaction area with a neighboring crab was a measure of *competition intensity*. Thus, with this

approach the strength of competition of a crab (i.e. the capacity to increase the *competition intensity* on other crabs) was constant at any point with distance r of this crab. The overlap areas of all the neighboring crabs were summed ($\sum Ov$) and divided by the interaction area of the focus crab (A_{int}) to evaluate its probability of movement:

$$P_{move} = \frac{C_Z \times \sum Ov}{A_{int}} \quad (8.4)$$

where C_Z was a scaling constant to obtain a wanted mean frequency of movement of the population (further explanations in “parameterization” part below, and see Table 8.1 for values). This handling of competition could be seen as simulating an identical probability of harvesting leaves or interacting directly with the neighbors on the entire interaction area of the crab. In term of behavioral interpretation, the crabs could be considered as giving the same importance to all resources on the interaction area.

Decreasing intensity competition submodel (RM_{FON}): This sub-model was adapted after the Field Of Neighborhood (Berger and Hildenbrandt 2000, 2003) and was the original competition model in Chapter 7. The strength of competition of an individual in its zone of interaction was considered at any point with distance r from a given crab as following the function $FON(r)$ described as:

$$FON(r) = \left\{ \begin{array}{ll} 1 & \text{for } 0 \leq r < CW/2 \\ \exp\left(-\frac{|\ln(F_{min})|}{R_{int}-CW/2} \times \left(r - \frac{CW}{2}\right)\right) & \text{for } CW/2 \leq r \leq R_{int} \\ 0 & \text{for } r > R_{int} \end{array} \right\} \quad (8.5)$$

where F_{min} was an arbitrary minimum competition strength (0.01) at R_{int} . This FON function could be described as the decreasing pressure that an individual create on the food resources going away from its burrow position. Thus, I considered the *competition intensity* affecting a focus crab as the sum of integrals of the FON intensity of the neighbors over the overlaps of their interaction area (defined as F_A , see Chapter 4, 5 or 7 for more precisions) divided by the area of interaction (A_{int}) representing the needed resources. This *competition intensity* (F_A/A_{int}) was then transformed into *competition effect* as for the other sub-models:

$$P_{move} = \frac{C_F \times F_A}{A_{int}} \quad (8.6)$$

where C_F was a scaling constant to obtain a wanted mean frequency of movement of the population (further explanations in “parameterization” part below, and see Table 8.1 for values). The corresponding hypothesis of behavior

Table 8.1: Parameter values of constants C in equations 8.3 (RM_{DENS}), 8.4 (RM_{ZOI}) and 8.6 (RM_{FON}) for the different values of constant a in calculation of R_{int} (Eq. 8.2)

	RM_{DENS}	RM_{ZOI}	RM_{FON}
$a=5$	$C_N=755.98$	$C_Z=0.224$	$C_F=1.864$
$a=10$	$C_N=439.19$	$C_Z=0.066$	$C_F=0.687$
$a=19$	$C_N=376.06$	$C_Z=0.025$	$C_F=0.279$

of crabs would be that they compete through interference or exploitation activity giving more importance to the closest resources than the one further away on the interaction area.

Parameterization of the sub-models

Each of these sub-models were tested with three constants a in the radius of interaction calculation (Eq. 8.1), corresponding to testing different importance of proximity areas around the individuals influencing decision of movement. To be able to compare the effect of these combinations (from now on, called “models”) on the focus patterns at population level, but limiting the number of other independent factors influencing these patterns, I considered that each model parameterization should lead to an arbitrary mean value of frequency of movement of crabs (f , calculated as the total number of movements done by all crabs during a period of time divided by this time period and number of crabs) for a given density (individuals.m⁻²), mean size of the crabs and size of radius of interaction (depending on parameter a). Thus, for each of the models using competition sub-models (not the RM_r), preliminary simulations were run with fixed crab density and mean crab size (Table 8.2, column a) to find the corresponding scaling constant C (in equations 8.3, 8.4 or 8.6) obtaining a mean frequency of movement of the crabs of $f= 0.07$ movement.crab⁻¹.day⁻¹. I decided to take this arbitrary value of $f = 0.07$ movement.crab⁻¹.day⁻¹ because it is approximately the one leading to the best reproduction of the field patterns of recovery in Chapter 7. Table 8.1 gives the C values with the corresponding radius calculation and competition sub-model. For the null model (using RM_r) P_{move} was set to 0.1 to obtain a mean frequency of movement of crabs of 0.07 movement.crab⁻¹.day⁻¹ because of the proportion of crabs staying in a closed burrow each day (cf Appendix A , page 218 for calculation).

Table 8.2: Parameters entering in the four types of simulations of IBU for each of the 28 models: 2 simulations with column a for the recovery pattern reproduction, 1 simulation with column b for the reproduction of the spatial distribution pattern, and 1 simulation with column c for the analysis of frequency of movement correlated with size. The use of individual parameters of probability of action (P_x) is described in Chapter 7.

Parameter	Description	a)	b)	c)
(X_{max}, Y_{max})	Size of the simulation area (in m)	(15, 15)	(7, 5)	(7, 5)
Max_{time}	Time length of simulation (days)	(10 +) 50 or 15	100	100
Dc	Crab starting density (in $/m^2$)	3.16	6.2	3.16
$PropUnoc$	Proportion of unoccupied burrows at start	22%	22%	22%
$PropClosed$	Proportion of closed burrows at start	60%	60%	60%
CW_{pop}	Mean carapace size of the simulated crab population (in cm)	6.5	5	6.5
$SD_{CW_{pop}}$	Standard deviation of the mean carapace size of the simulated crab population (in cm)	2.5 *	1.0	2.5
P_{c1}	Probability of taking over an occupied burrow	0.0	0.0	0.0
P_{c2}	Probability of taking over a closed empty burrow	0.05	0.05	0.05
P_{c3}	Probability of taking over an open empty burrow	1.0	1.0	1.0
$P_{closing}$	Probability that a crab closes its burrow at each time step	0.14	0.14	0.14
$P_{opening}$	Once closed, probability of opening its burrow at each time step	0.33	0.33	0.33

* The $SD_{CW_{pop}}$ was in column a) the only different parameter to Chapter 7 to simulate a population with more different sizes

8.3.2 Simulations

Population-level patterns

Each of the 9 competition models (3 sub-model \times 3 sizes of radius of interactions) and the model using the null sub-model (altogether hereafter referred to as the 10 models) were tested to reproduce three field patterns at population level (Table 8.3). 3 simulations with 30 replicates each were run to evaluate the reproduction of these three field patterns. They consisted of: the data points of proportion of recovered number of burrows taken from the two experiments of recovery of entirely fished areas (with or without removing burrows) described in Chapter 7 (Fig. 7.1, page 169, the data points but not the regression lines); and the spatial distribution pattern evaluated with the L-Ripley function at individual-level showing regularity at small scale ($\sim 25\text{cm}$) described in Chapter 6 (Fig. 6.2g, page 149, but only on the scale of r between 0 to 50cm). The two first simulations were run with the parameters presented in Table 8.2 (column a), and with a scheduling as described in Chapter 7: 10 steps after the initialization of the simulations, the crabs of a center area of 12.35m^2 were removed. The recovery was evaluated during 50 and 15 days (corresponding to the 2 experiments respectively) as the proportion of crabs re-installed in the fished area compared to the original density before removal. The third simulation was run with different parameters (Table 8.2 column b) to simulate this time a small area with local density and crab size corresponding to the small scale map of $3\times 5\text{m}$ described in Chapter 6. These simulations were run for 100 time steps during which no crabs were removed. The spatial distribution of the crab positions were evaluated after these 100 days with an L-Ripley function on a center area of 15m^2 as described in Chapter 6 (Eq. 6.1 and 6.2, page 145).

Competition symmetry

The differences of way of measuring *competition intensity* among the three sub-models (equations 8.3, 8.4 and 8.6) were assumed to develop different degree of size-symmetry competition. For the RM_{DENS} sub-model, the density around the focus crab was the measurement of *competition intensity*. Thus, the *competition effect* should be size-independent. This size-independent effect could be expressed as simulating a proportional share of resources depending on their needs. Consequently, I expected that this RM_{DENS} sub-model simulated symmetric competition. For the other two sub-models, previous studies gave these assumptions. Weiner et al. (2001) considered a ZOI model simulating resource partitioning with a rule of equal share among overlapping individuals. However, they stipulated that an inherent char-

Table 8.3: Description of field patterns (*Obs*) and corresponding simulation values (*Sim*) considered in the analysis of goodness of fit of the different models (N_{obs} = number of points to reproduce).

Patterns	N_{obs}	<i>Obs</i>	<i>Sim</i>
Recovery experiment 1 (REC1)*	18	Values of proportion of density recovered (at different time after fishery)	Simulation values of proportion of density recovered
Recovery experiment 2 (REC2)*	30	Values of proportion of density recovered (at different time after fishery, and from different plots)	Simulation values of proportion of density recovered
Spatial distribution (SPAT)	10	L(r) Ripley function of 3x5m map of Chapter 6 for $r=[5,50]$ cm	L(r) Ripley function of simulation results after 100days for $r=[5,50]$ cm

* Note that the recovery patterns in this study are the original points of recovery proportion and not the linear regression as in Chapter 7.

acteristic of ZOI models is that a partial size-asymmetry occurs with such configuration, because the larger of 2 competing individuals has always a lower percentage of its area under share than the smallest individual. Thus I expected the RM_{ZOI} sub-model to create partial asymmetric competition. Bauer et al. (2004) argued that the FON approach should create asymmetric competition conditions. Thereby, I expected the RM_{FON} sub-model to create also asymmetric competition.

To test these assumptions, a simulation for each of the 10 models (with the additional parameters described in table 8.2 column c) was run to record the final number of movement that each crab had done during 100 time steps. I chose here to simulate an identical crab population than in the recovery experiment, but without removal of individuals (hence the additional simulations). Using the competition sub-models, the probability of movement is directly dependent on the effect of competition. This *competition effect* was the expression of a *competition intensity* felt by the individuals. If the effect of competition is higher for small individuals than big ones, the frequency of movement of the former should be higher than for the latter. It would also mean that the resources were simulated as not proportionally shared since the *competition effects* were set as independent on the resource need (supposed by the division by A_{int} in equations 8.3, 8.4 and 8.6). Thus, for each model, I analyzed if a significant correlation between the number of move-

ments done by each crab and their sizes existed and with what sign (positive or negative). For verifying the significance of the correlation, a simple linear regression analysis with analysis of variance on the parameters of the regression model was effectuated. I could estimate out of these correlations if a model led to more movements of small or big crabs, or if there was no significant trend among sizes. I interpreted a significant negative correlation as a sign of asymmetric competition in favor of big crabs. On the other hand, a significant positive correlation was seen as a sign of asymmetric competition in favor of small crabs. A lack of significance was seen as a symmetric competition situation.

8.3.3 Analysis of goodness of fit to the patterns

For the assessment of reproduction of the three patterns for each of the 10 models I used two approaches: a mean-square deviation method (a bit different than in Chapter 7) and the Pattern-Oriented Modeling Information Criterion (*POMIC*) approach described in Chapter 2. For each of these two criteria of goodness of fit, a first calculation evaluated how well each pattern was reproduced, and a second evaluated the total goodness of fit of the model to the 3 patterns together assuming that each pattern had the same importance.

The mean square-deviation (*MSD*) was calculated for each pattern as:

$$MSD = \frac{1}{30 \times N_{obs}} \sum_{r=1}^{30} \sum_{t=1}^{N_{obs}} (Obs - Sim_2)^2 \quad (8.7)$$

where *Obs* was the field observations, *Sim* was the corresponding simulation results of the replicate *r* and N_{obs} was the number of field observations (Table 8.3). A total deviation error (Tot_{MSD_i}) was calculated as:

$$Tot_{MSD_i} = \frac{1}{3} \sum_{j=1}^3 \frac{MSD_{j,i}}{\min MSD_j} \quad (8.8)$$

where *i* was the model considered, *j* indicated the pattern and $\min(MSD_j)$ was the minimum value of *MSD* for the pattern *j* of all our 10 tested models.

The *POMIC* calculation was also used to indicate the goodness of fit for each pattern. For each of the 10 models, the simulation results of the 30 replicates were combined per observations for the corresponding Obs_t (the t^{th} observation of the field pattern) in a vector of 30 values $VSim_t$ of range Sim_{range} . This vector was first transformed with a Gaussian density kernel estimator (R Development Core Team 2006) of band width (*bw*) approximately equal to a tenth of the difference between the bigger and smaller

values of $Vsim_t$. The resulting densities (vector Ds) were then scaled into probabilities of observation (Ps). This was done by dividing Ds by the maximum probability value estimated from the frequencies of observations in the vector $Vsim_t$ divided in classes of widths bw . The Ps values were always 512 values (standard of the R Gaussian kernel density estimator) corresponding to a vector $PSim$ of 512 hypothetical Sim values of range $PSim_{range} = [\text{minimum value returning a } Ds > 0, \text{ maximum value returning a } Ds > 0]$ and of constant increment (maximum-minimum /511). The likelihood of a model to have reproduced a field observation $L(Obs_t|model)$ was then determined as:

$$L(Obs_t|model) = \left\{ \begin{array}{ll} Ps[k] & \text{if } Obs_t \in PSim_{range} \\ 1.09 \times 10^{-314} & \text{otherwise} \end{array} \right\} \quad (8.9)$$

where k was the position in vectors Ps or $PSim$ where $PSim[k]$ was the closest to Obs_t . The $1.09e-314$ value was an arbitrary value close to zero given to the likelihood when the simulation range (Sim_{range}) was not close enough to the field observation (Obs_t) to have a $Ps > 0$. It was set to avoid getting infinite values of $POMIC$ (because of the logarithm function in $POMIC$, see below). The number of time this occurred was however kept in a variable (Nun) to count the number of time the considered model had its simulation results not covering the field observations. The goodness of fit indicator for each model i was then calculated as:

$$POMIC_i = -\frac{1}{N_{obs}} \sum_{t=1}^{N_{obs}} \log(L_i(Obs_t|model)) \quad (8.10)$$

The $POMIC$ approach was also used to inform about the total goodness of fit of each of the 10 models to the three patterns considered together. According to Chapter 2, this total goodness of fit was calculated as the mean $POMIC$ of the three patterns:

$$Tot_{POMIC_i} = \frac{1}{3} \sum_{j=1}^3 POMIC_{i,j} \quad (8.11)$$

where i was the considered model and j indicated one of the three patterns. The advantage of this approach compared to Tot_{MSD} was that the total goodness of fit for one model was independent of the goodness of fit of other models. Additionally, the Tot_{POMIC} criterion kept a track of the number of time the simulation results did not range such that the corresponding observation value fell within or close to them. Note that all $POMIC$ values (or Tot_{POMIC}) should be considered in term of their differences to the smallest one. In general, it can be assumed that when this difference is < 1 , the

corresponding model is at as high evidence as the best model (Chapter 2). For the final goodness of fit indicator, the differences of Tot_{POMIC} (Δ_i) were calculated:

$$\Delta_i = Tot_{POMIC_i} - Tot_{POMIC_{min}} \quad (8.12)$$

where the $Tot_{POMIC_{min}}$ was the minimum Tot_{POMIC} value among all 10 models. These differences were used to compute the probability of a model to be the best one among the set of 10 (Chapter 2):

$$W_i = \frac{\exp(-\Delta_i)}{\sum_{r=1}^{10} \exp(-\Delta_r)} \quad (8.13)$$

All analyses were effectuated with scripts developed for the R software ©version 2.3 (R Development Core Team 2006).

8.4 Results

Mean frequencies of movement of crabs were measured as ~ 0.07 movement.crab⁻¹.day⁻¹ for most models (Table 8.4, column Freq). Only the RM_{ZOI} sub-model of competition with small radius of interaction (parameter $a=5$) resulted in frequency of movement > 0.075 movement.crab⁻¹.day⁻¹.

The correlations among crab size and number of movement for simulations using the RM_{DENS} sub-model showed a different trend of correlations with the different values of the parameter a for the radius of interaction calculation (Table 8.4, column Sign). With small and intermediate radius of interaction, the correlations showed positive signs, indicating a significant higher number of movements of big crabs than small ones. With large radius of interaction ($a=19$) the correlation led to non-significant difference of number of movement. Simulations using the two other sub-models of competition obtained always the same patterns of correlations across the different radius of interactions. The RM_{ZOI} sub-model led always to significantly higher number of movement of small crabs than big ones. With the sub-model using the FON approach, the correlations led to non-significant differences of number of movement among sizes. The null model using the RM_r sub-model led also to a non-significant difference of number of movement among sizes.

The first pattern of recovery was best reproduced with the RM_{ZOI} sub-model according to both indicators (table 8.4 columns REC1), although not with identical radius of interaction. All models had simulation results including all field observation points in their range (table 8.4, column $Nun=0$ in REC1). Most $POMIC$ values (9 out of 10) showed differences to the smallest $POMIC < 1$. This indicated that the evidence of reproduction of this

Table 8.4: Results of each model in frequency of movement of crabs (Freq), sign of correlation crab size vs. frequency of movement (Sign) and indicators of goodness of fit for each pattern (REC1, REC2 or SPAT). a = Values of a in R_{int} calculation, MSD = mean square deviation (Eq. 8.7), $POMIC$ = Pattern oriented modeling information criterion (Eq. 8.10), Nun = Number of non-reproduced observations by the simulations. The best results of MSD or $POMIC$ for each considered patterns are indicated in **bold**. In the $POMIC$ columns, models having less evidence than the best one are in grey ($POMIC$ differences > 1). † indicates the model selected to show on Fig. 8.1 the reproduction of the recovery patterns (REC1 and REC2), ‡ indicates the model selected to show on Fig. 8.2 the reproduction of the spatial distribution pattern (SPAT).

a	Sub-model	Freq	Sign	REC1			REC2			SPAT		
				MSD	$POMIC$	Nun	MSD	$POMIC$	Nun	MSD	$POMIC$	Nun
5	RM_{DENS}	0.073	+	1.224	2.289	0	0.982	26.599	1	285.697	2.610	0
	RM_{ZOI}	0.086	-	0.892	1.071	0	0.708	49.971	2	178.725	1.918	0
	RM_{FON}	0.067	=	0.539	1.534	0	0.799	49.965	2	107.605	1.909	0
10	RM_{DENS}	0.069	+	0.642	1.625	0	0.850	50.279	2	168.093	1.797	0
	RM_{ZOI} †	0.070	-	0.439	1.236	0	0.922	26.044	1	222.452	2.241	0
	RM_{FON} ‡	0.068	=	0.481	1.354	0	0.781	50.247	2	111.915	1.653	0
19	RM_{DENS}	0.070	=	0.550	1.368	0	0.906	50.780	2	274.345	2.593	0
	RM_{ZOI}	0.069	-	0.527	1.303	0	0.825	26.055	1	324.496	74.672	1
	RM_{FON}	0.069	=	0.482	1.412	0	0.829	26.455	1	209.164	2.707	0
	RM_r	0.068	=	0.821	1.762	0	0.856	26.200	1	490.818	3.922	0

pattern was the same for all these 9 models. The second pattern of recovery was also best reproduced with the RM_{ZOI} sub-model according to both indicators (table 8.4 columns REC2). Five models had equivalent evidence of goodness of fit than the best one according to the $POMIC$ differences. The $POMIC$ values also indicated that the Null sub-model of interaction (RM_r) was better in reproducing this pattern than many of the models using competition sub-models. The field observations were not reproduced entirely with any model (table 8.4, column $Nun > 0$ in REC2), with at least one field observation always not reproduced. The pattern of spatial distribution at small scale was best reproduced by the RM_{FON} sub-model according to both indicators (table 8.4 columns SPAT), although not with identical radius of interaction. A set of 3 models, including the one using the RM_r sub-model, had less evidence of reproducing the pattern than the best model according to the $POMIC$ values (difference > 1). The figures 8.1 and 8.2 show the best models that reproduce respectively the recovery patterns (REC1 and REC2) (RM_{ZOI} with $a=10$, see Table 8.4) and the spatial distribution at small scale (SPAT) (RM_{FON} with $a=10$, see Table 8.4).

The Tot_{MSD} indicator of total goodness of fit of the three patterns together indicated that overall, the best assumption of interaction to use was the RM_{FON} sub-model (Table 8.5) with intermediate ($a=10$) radius of inter-

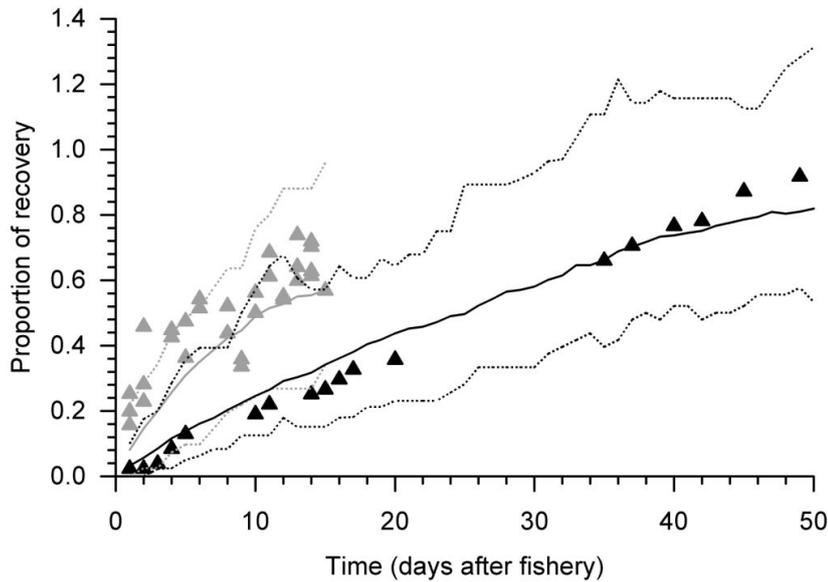


Figure 8.1: Reproduction of the recovery after fishery of the most realistic model for this pattern (RM_{ZOI} with $a=10$, selected in Table 8.4) (Solid black and grey lines: mean of proportion of recovery after fishing from 30 simulations experiment, with removing the burrows or leaving the burrows respectively; black and grey dashed lines: corresponding maximums and minimums; black and grey triangles: respective field patterns of recovery (REC1, REC2), c.f. Fig 7.1).

action. A set of 4 models had differences of Tot_{POMIC} to the best fit <1 , indicating a potential equivalent evidence of being the best model to all of them. The weights of evidence outlined that the best model, the RM_{ZOI} with intermediate size of interaction area, had a probability to be the best model <0.90 . The model using the RM_r sub-model received the lower weight of evidence of this set of models that obtained range of simulation results covering all but one field observation (in pattern REC2).

8.5 Discussion

This study used the Individual-based *Ucides cordatus* model (IBU) to test different models of individual-level competition in reproducing 3 patterns observed at population level. The results illustrated that a model simulating the effect of competition among neighbors as initiating force of movement reproduce better all population-level patterns than a null model considering random reason of movement. The results are also showing a trend of higher importance of resources close to the burrows in triggering individual movement. The influence and importance of asymmetric competition is however

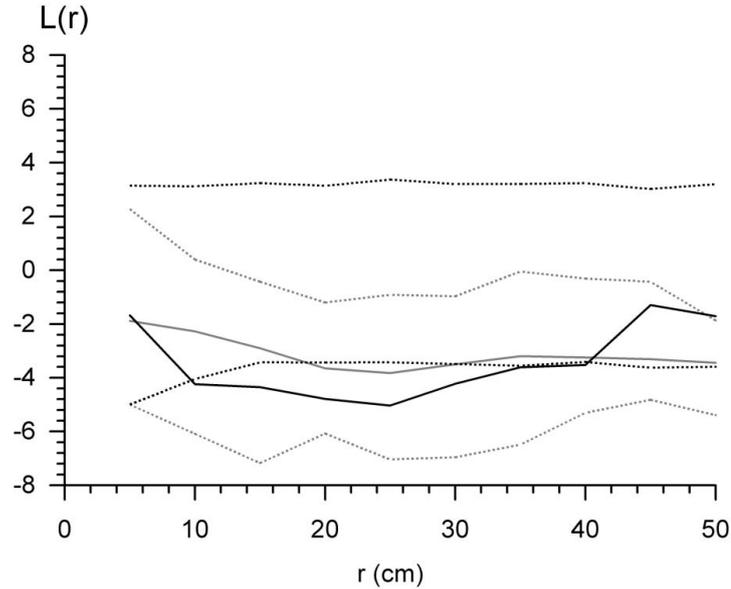


Figure 8.2: Reproduction of the spatial distribution pattern at small scale with the most realistic model for this pattern (RM_{FON} with $a=10$, selected in Table 8.4) (Solid black line: L-Ripley function of the field observations; black dashed lines: 95% confidence envelope for complete spatial randomness (CSR) using 999 Monte Carlo randomizations (c.f. Fig 6.2g); solid grey line: mean L-Ripley function from 30 simulations experiment; grey dashed lines: corresponding maximums and minimums).

harder to estimate.

8.5.1 Model structure and symmetry of competition

The Chapter 7 argued that the frequency of movement of individuals was one of the most important factors to reproduce the recovery patterns of *U. cordatus* populations observed on mangrove forest of North-Brazil. In the present study, each model version was configured to reproduce an overall identical frequency of movement ($0.07 \text{ movement.crab}^{-1}.\text{day}^{-1}$). Particularly, the models using a competition sub-model were parameterized from preliminary simulations to assure that the overall *competition intensity* would be transformed into probabilities of movement of individuals leading to the wanted overall mean frequency of movement. Only the sub-model using the zone of influence approach with small radius of interaction led to frequencies of movement a bit too high, but still within a range that was defined as biologically acceptable in Chapter 7 ($<0.14 \text{ movement.crab}^{-1}.\text{day}^{-1}$). It might have influenced the results of goodness of fit since this model was seen as among the best reproducing the recovery patterns. However, it did

Table 8.5: Results of each model in overall indicators of goodness of fit: Tot_{MSD} = total mean square deviation (Eq. 8.8), Tot_{POMIC} = total pattern oriented modeling information criterion (Eq. 8.11). The orders show the “best” (1, in **bold**) to the “worst” (10) fitting model according to the respective criterion (Tot_{MSD} or Tot_{POMIC}). The weights of evidence are calculated from Tot_{POMIC} values (Eq. 8.13) and can be seen as probability to be the best model (a = values of a in R_{int} calculation, **grey** values of Tot_{POMIC} indicate differences to the best model > 1).

a	Sub-models	Tot_{MSD}	Tot_{POMIC}	$OrderTot_{MSD}$	$OrderTot_{POMIC}$	Weight of evidence
5	RM_{DENS}	2.315	10.499	9	3	0.193
	RM_{ZOI}	1.592	17.653	6	5	0.000
	RM_{FON}	1.136	17.802	2	7	0.000
10	RM_{DENS}	1.429	17.901	4	8	0.000
	RM_{ZOI}	1.470	9.840	5	1	0.373
	RM_{FON}	1.095	17.751	1	6	0.000
19	RM_{DENS}	1.711	18.247	7	9	0.000
	RM_{ZOI}	1.810	34.010	8	10	0.000
	RM_{FON}	1.419	10.191	3	2	0.263
	RM_r	2.573	10.628	10	4	0.170

not lead to overall better evidence to reproduce the three patterns together. This small error in parameterization should therefore be kept in mind for the inference on the role of asymmetry and distance of resources.

The change of symmetric competition type with the simplest competition sub-model (RM_{DENS}) can be explained from the models' structures. The large radiuses produced a symmetric competition situation as expected for this sub-model. The two other radiuses showed asymmetric competition in favor of small individuals. With parameterization of large radiuses of interaction, the *competition effect* that an individual feels is depending less on the local variation of density than with intermediate and small radiuses. The small and intermediate radiuses of interaction parameterization lead to higher variability in estimating the density. This is transformed to higher variability in *competition intensity* estimation and thereby higher variability of probability of movement for each crab than with the large radius of interaction. Additionally, considering an identical density around a small individual, this density might be under-estimated to be 0 with small radiuses of interaction. In this case, the probability of movement becomes then equal to 0. By increasing the overall variability of probability of movement but cutting its distribution on its lower end, these smaller radiuses of interactions are creating a distribution of number of movement depending on the number of times each individual had an estimation of density on its interaction area equal to 0. Thus, the smaller the radius of interaction, the more the competition becomes asymmetric in favor of small crabs. This characteristic of the density-based competition models (using RM_{DENS}) should lead to prefer an

interaction radius corresponding to the field observations than with smaller ones. This would insure the symmetry of competition to be dependent on the competition sub-model and not the size of the radius of interaction.

For the two other competition sub-models, the trends of correlation sign, and thereby the assumed type of competition symmetry was not different among the three radiuses of interaction parameterizations. The models using the ZOI sub-models led to the expected partial asymmetric competition whereby small crabs are more influenced by identical *competition intensity* than big crabs. Weiner et al. (2001) considered a ZOI model simulating resource partitioning. Their ZOI model could not reproduce perfect symmetry and apparently this ZOI characteristic forced them to compare partial size-asymmetry (according to Schwinning and Weiner 1998) to total asymmetry where the big individual takes all resources in overlap situation. In the case of the present study, I did not consider mechanistic resource partitioning with any of the sub-models, but a phenomenological *competition intensity* and transformation to *competition effect*. Assuming that the correlation among size and number of movement is a good indicator of competition symmetry, my study shows that a phenomenological approach leads to identical results than the more mechanistic one of Weiner et al. (2001).

The types of competition assumed with the FON sub-models led to apparent competition symmetry with all the radius of interaction. This goes against the expectations of Bauer et al. (2004) who used a measure of *competition intensity* as in the present study. However, an explanation might come from the fact that the model of Bauer et al. used a different formula to estimate the *competition effect* than the one used here (here: *competition effect* = constant transforming factor \times *competition intensity*). They calculated this *competition effect* by taking the maximum among 0 and 1-*competition intensity* as in the KiWi model (Berger and Hildenbrandt 2000). This may lead to a threshold situation where increase in *competition intensity* would not increase the *competition effect* (see also Appendix B, page 219 for further argumentations). At least, these differences of approaches could be confirmed with analytical mathematical development (not easily solvable) of the two different ways. An interesting finding coming from my results with IBU would be then that the impossibility to have perfect symmetry (Schwinning and Weiner 1998) under a ZOI approach (as seen above) could be given by the FON approach for further studies on symmetry effect on plant populations.

8.5.2 Differences in methods analyzing the reproduction of population-level patterns

The results of pattern of recovery reproductions by the different model versions were relatively complementary to the observations of Chapter 7. The measure of goodness of fit with the mean square deviation (*MSD*) confirmed that the model version with the sub-model of random reason for movement had a worse fit than the model using the original FON approach as in Chapter 7. However, the results of the pattern-oriented modeling information criterion (*POMIC*) approach demonstrated that the evidence of the competition models was not higher than for the null model as to be reproducing the processes leading to the recovery patterns. Although speaking of significance with information criteria is not recommended (see e.g. Burnham and Anderson 2002), these results could be interpreted in simpler words as a lack of significant difference among the null and the competition models for the reproduction of these 2 first patterns. However, this does not contradict the findings of Chapter 7 that competition would be the trigger of crab movement leading to recovery of fished areas. This, mainly because the Chapter 7 analysis focuses on trying to reproduce the linear aspect of the recovery and not only the data points as I did here.

The *MSD* results showed that the null model was not reproducing the spatial pattern at small scale as well as all the other models. The *POMIC* approach gives additional insights in term of evidence of the models to fit the specific spatial pattern. Its results show that it is possible that the null model of reason of movement reproduce all points of observation. However, the goodness of fit of this model is such that the *POMIC* differences demonstrate a much lower evidence of being a good model reproducing the process underneath the spatial pattern than the best competition models using the FON approach. Thus, the *POMIC* help in being secured that the competition model should be preferred in term of goodness of fit.

Considering the three patterns together and of equal importance, the *MSD* and *POMIC* indicate different best sub-models to use to simulate crab interactions. These differences come mainly from the sensitivity that *POMIC* gives to the overall range of simulation results that should cover as much as possible the field observations points. *POMIC* is also dependent, as the *MSD*, on the distance of the simulation results to the observation points (through the likelihood function that returns lower values (leading to higher *POMIC*) as the simulations results are further away from the field observations). But the additional characteristic of *POMIC* makes for example that the best model according to *MSD* is found at the 6th position with *POMIC* and with a weight of evidence of 0 as to be a good model

reproducing the patterns. *POMIC* also informs that overall the null model is having a 17% probability of being a good model reproducing the three patterns together given the set of model tested in the present study. This is much higher than many other model versions, but less than half the evidence of the best model with ZOI.

8.5.3 Competition at individual level and inferring on individual behavior

Although the *POMIC* approach showed that overall the intraspecific competition among individuals is not necessarily the phenomenon leading to the observed recovery patterns, this study confirm the hypothesis that it is at the origin of the spatial pattern of organization. Both goodness of fit indicators, *MSD* and *POMIC*, showed a better reproduction of the spatial pattern with models simulating competition, and particularly the one implying the degree of importance of resources according to their distances (FON). Additionally, all the models that had evidence to reproduce this pattern were considering small or intermediate radius of interaction. Thus to reproduce this pattern, the close-by resources (food and/or territory) were seen much more important than further ones for the crab to decide to move. These confirmed the expectation of Chapter 6 that there is probably a repulsion process among crabs through competition for space and food that lead to the regular organization observed at small scale. These conclusions can be compared to the effect of competition among growing trees leading to a regular spatial organization (e.g. Kenkel 1988).

Considering all patterns together, the radius of interaction used by the best fitting models of each competition sub-models types (DENS, ZOI or FON) helped in inferring on the presence or not of a spatial preference of *U. cordatus* in resources. The simplest model (DENS) measuring *competition intensity* as directly linked to density showed a much higher importance of the closest resources for a crab to decide if it should move or not. The second simplest model (ZOI) reproduced better the field patterns with an intermediary radius of interaction, implying an importance of the resources closer to the burrow than the originally believed radius of harvest. The best FON model used the largest interaction radius. This confirmed the previous observation of higher importance of resources close to the burrow. This FON model can also be interpreted as a new hypothesis that further away resources might not be competed for with a territorial behavior, but better through indirect exploitation competition. This would have to be verified with mechanistic models simulating clearly territorial or exploitation

behaviors. All models indicate that the most important resources are the ones close to the burrow, and that too high *competition intensity* on these resources might lead a crab to take the decision of changing burrow. The sizes of zone of harvest assumed in Chapter 7 are therefore the extreme largest possibilities and in general *U. cordatus* would use smaller areas.

Finally, the results of the best fitting model of this study (RM_{ZOI} with intermediary radius) also argue in favor of the hypothesis that big crabs have more influence in excluding small individuals than their equivalent share of the resource. This would explain more easily the observations of Diele (2000) and Chapter 6 illustrating that small crabs are excluded from best habitats toward peripheral habitat by few big crabs. However, this trend only arrives considering all the patterns together. When considered individually, no indication let believe preferentially that asymmetric (ZOI) or symmetric (FON, and large radius DENS) competition is happening among individuals. The movements that lead to the recovery pattern might have a tendency to be more due to asymmetric competition, although the differences of evidence do not let conclude surely about it. Identically, the movements that lead to the regular spatial organization at small scale are only a little bit more likely to be caused by a symmetric competition than by an asymmetric competition. Further field work documenting the relationship among frequency of movement of crabs and their size could determine whether asymmetric or symmetric competition occurs with the help of the present findings. At least, these could give new patterns to be fit by the models, and thus help in inferring on the other aspects of intraspecific competition in *U. cordatus* populations.

To conclude, this study touched several aspects on analyzing competition models with a pattern-oriented modeling approach. First, it illustrated the capacity of *POMIC* to help in a situation of strong inference on models fitting several patterns. It confirmed the observation of Chapter 7, with one pattern more (the spatial pattern) that competition for resource might be at the origin of crab decision to change burrow. It illustrated the importance of the way of describing the transformation of *competition intensity* into *competition effect* in individual-based phenomenological competition models to produce different type of competition symmetry. And finally, this analysis of competition symmetry showed also the need of new field work to investigate the trend of frequency of movements among crab size classes.

8.6 Acknowledgements

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8.8 Appendices

8.8.1 Appendix A. How to parameterize the P_{move} value to obtain a mean frequency of movement of 0.07 movement.crab⁻¹.day⁻¹ for the null sub-model RM_r .

I want to obtain a precise mean frequency of movement of all the crabs with each sub-models ($f = 0.07$ movement.crab⁻¹.day⁻¹). The null sub-model (RM_r) is the simplest one to parameterize for that since it depends only on the proportion of open burrows and the parameter P_{move} . The mean frequency of movement (in movement.crab⁻¹.day⁻¹) is the results of an approximately constant proportion of moving individual at each day (x , thus I want $x=7\%$). At each time step, only the crabs with an open burrow will potentially move, so we have overall:

$$x = P_{move} \times Pop \quad (8.14)$$

where Pop is the proportion of open burrows. I just need to estimate what would be this proportion of open burrows to find what should be P_{move} . After several time steps, when the proportion of open burrows is not depending on the original settings, Pop is dependent on the individual behaviors, i.e. the probability of a crab to open its closed burrow ($P_{opening}$, table 8.2) or close its opened burrow ($P_{closing}$, table 8.2). This should be at first:

$$Pop = \frac{\text{Open burrows}}{(\text{Open Burrows} + \text{Closed burrows})} = \frac{N_O}{N_O + N_C} \quad (8.15)$$

Considering at each time step that Open burrows (N_O) are the ones already open not changing + the ones going to open from the Closed burrows (N_C), you have:

$$N_O \text{ at } t_1 = N_O \text{ at } t_0 \times (1 - P_{closing}) + N_C \text{ at } t_0 \times P_{opening} \quad (8.16)$$

So that after enough time steps a stable situation can be expressed as:

$$N_O \approx N_O(1 - P_{closing}) + N_C \times P_{opening} \quad (8.17)$$

Which can be re-wrote:

$$1 \approx (1 - P_{closing}) + (N_C/N_O) \times P_{opening} \quad (8.18)$$

Or :

$$P_{closing}/P_{opening} \approx N_C/N_O \quad (8.19)$$

So changing 8.15 in term of N_C/N_O , I have:

$$1/Pop = (N_O/N_O) + (N_C/N_O) = 1 + P_{closing}/P_{opening} \quad (8.20)$$

Which gives then:

$$Pop = P_{opening}/(P_{opening} + P_{closing}) \quad (8.21)$$

So, I can calculate directly what should be P_{move} for a specific x (and thereby f):

$$P_{move} = x \times \frac{(P_{opening} + P_{closing})}{P_{opening}} \quad (8.22)$$

Since we want $x = 0.07$, and we set $P_{opening}$ and $P_{closing}$ in table 8.2, we obtain P_{move} to be approximately 0.1.

8.8.2 Appendix B. Why the asymmetric competition demonstrated by Bauer et al (2004) might not be coming from the FON approach at individual level?

Bauer et al. check for competition asymmetry at 2 levels: population level with an index (from Wyszomirski) and individual level assuming that the asymmetry would be visible in either:

1. The trajectory of the *competition intensity* (their variable F_A) and an un-scaled *competition intensity* ($F = F_A \times A_{ZOI}$ where A_{ZOI} is the zone of influence area) during the growth of two interacting individuals.
2. The difference (D) in relative growth rates (S) given by $D = |S_1 - S_2|$ with $S = \frac{GR - \Delta R_{basal}}{GR} = 1 - C$ where GR is the growth rate without *competition effect* (depending on R_{basal} , = the size of the tree), ΔR_{basal} is the growth rate with *competition effect* and C is the *competition effect* on the growth rate GR to obtain ΔR_{basal} .

The problem that I encountered comes from the individual level evaluation of asymmetry and explains the asymmetry observed at population level with the index.

Let's see first the argumentation of the second indicator of asymmetry: the difference in relative growth rates D . The authors assumed that D should be equal to 0 if the two plants were in symmetric competition situation. According to the definition the authors give on the first sentence:

“Asymmetric competition among individuals is defined as competition in which larger individuals have a disproportionate advantage (relative to their size, e.g. mass) over smaller individuals.”

in a symmetric competition situation between two individuals of different size, the *competition effect* of the first individual on the other (C_2) should be proportional to its size ($Size_1$):

$$C_2 = Constant \times Size_1 \quad (8.23)$$

And thereby, asymmetry could be assumed to occur in any situation where:

$$C_2 \neq Constant \times Size_1 \quad (8.24)$$

Thus, asymmetry should be evaluated as a difference of competition influence on growth in relation to the sizes. However, the D parameter does not include the “relation to the sizes” aspect.

If we take

$$S = 1 - C \quad (8.25)$$

then D is:

$$D = |(1 - C_1) - (1 - C_2)| \quad (8.26)$$

or

$$D = |C_2 - C_1| \quad (8.27)$$

With

$$C = 1 - 2F_A \quad (8.28)$$

we have:

$$D = 2 \times |F_{A_1} - F_{A_2}| \quad (8.29)$$

Thus, D is measuring the difference of *competition effect* (Eq. 8.27), but it does not check this in relation to the sizes. Or D measure the difference in FON integrations (different for the 2 individuals because of different sizes and differently away from the stem) divided by the ZOI areas (different for the 2 individuals because of different sizes) (Eq. 8.29). The 2 integrations of FON over the overlap areas are different (i.e. unscaled *competition intensities* are different), but the scaling done with the division of this FON integration by the ZOI area is not obviously leading F_A to give information on *competition intensity* relative to the size (it might be that the *(factor depending on size)/(factor depending on size)* division annul this required information). And thus, D is not obviously giving information on *competition effect* relative to the sizes of the 2 individuals.

In biological terms, I cannot interpret the integration of FON entirely and thus cannot conclude on the production or not of an asymmetric competition situation with the parameters given by Bauer et al. Only in the case that their I_{min} parameter is 1 (coming back to an original ZOI model) the FON integration would be equals, and then the division by the ZOI area to obtain F_A is surely giving size un-proportional *competition effect*, as argued by Weiner et al. (2001). But finally, a measure of asymmetry of competition should not be done with the *competition effect* measure itself. The relative growth rate could be a tool of comparisons among individuals and analysis of competition type, but relative to the size, not calculated relative to the competition. (e.g. Thomas and Weiner 1989, Including competitive asymmetry in measures of local interference in plant populations, *Oecologia* 80:349-355. They calculated the relative growth rate (RGR) as $RGR = (\text{Size at } t_2 - \text{Size at } t_1) / \text{Size at } t_2$).

The first argument of observation of asymmetry at individual level was a shift in the trajectory in size, F_A or F . Although based on assumptions not completely explained, a shift in trajectories could be assumed as a sign of asymmetry. Let assume this is true, but let also see where the shifts observed by the authors are coming from. In all their graphs (figure 5 and 6 of their paper), this shift occur when the F_A of the smaller individual reach 0.5, as mentioned in the result part of the paper. This threshold value is not because of a particularity of the intensity field in the FON, but from the use and calculation of the “competition factor” C measuring the *competition effect*, which is set to 0 when F_A reach 0.5. The authors set this value because of the way C is calculated: $C = 1 - 2 \times F_A$ so that if $F_A > 0.5$ the C would not become negative. But this value of 2 multiplying the F_A to transform *competition intensity* into *competition effect* (what I called the sharing capacity in Chapter 4) has no biological meaning on this article, neither a precise parameterization. It could take any value in a

theoretical study. Particularly, in a study of analysis of the FON reproduction of asymmetry among 2 individuals it should have been set to 1, so that the real effect of C on the trajectories would have been directly seen (and not the effect of a threshold). In such case the F_A of the 2 individuals would never reach 1 and C would always be >1 . The threshold not being met, there would have been no shift in trajectory. This was obtained by Bauer et al. with the low I_{min} simulation because the 2 individuals never obtained a F_A reaching 0.5. Bauer et al. used then the first criterion (relative growth rate) to argue that asymmetric competition was nevertheless visible in this case of low I_{min} . I believe it is not a secure indicator of asymmetry (cf. above), so I would conclude that the asymmetric competition occurring among the 2 plants because of the FON was not proved in this paper.

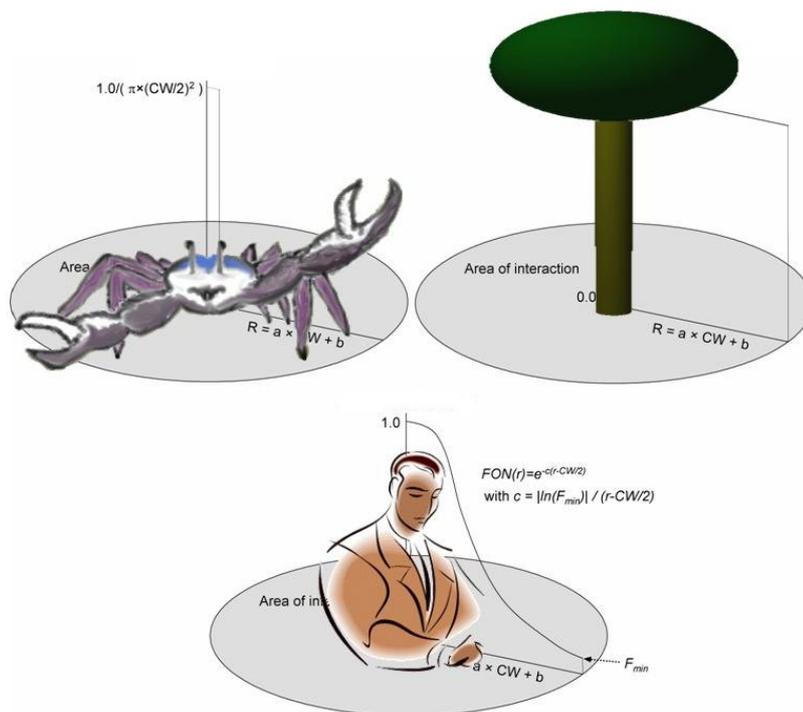
I believe however that the general approach of the simulation, using a factor of *competition effect* on growth as $C = \max(0, 1 - \text{Competition intensity})$ lead to asymmetry in general at the population level. The connection between the way of determining the *competition intensity* for each individual in a population of $n > 2$ individuals and the calculation of the *competition effect* is the key to asymmetry. With the above *competition effect* calculation, if the *competition intensity* value can get >1 for an individual, then because of the competition factor C calculation, sooner or latter individuals will reach $C=0$ and stop growing. The repressed individuals create then a clear difference in growth rates with the ones still growing (because not yet at $C=0$), which should be the bigger ones (as seen in their individual exercise). The overall situation present finally some plants much bigger than their neighbors that stopped growing much earlier because of their spatial constellation, which can be seen as asymmetry with the index used in Bauer et al. They measured *competition intensity* with the $2 \times F_A$ evaluated in a spatially explicit way, and could get easily values >1 . Thus, asymmetry appeared at population level. This result is very interesting and still valuable, but to my opinion, because of the description at individual level, I believe it is not because of the FON approach itself, but because of the C calculation chosen given the way of estimating *competition intensity*.

If Bauer et al. meant by the “FON approach” the entire way of simulating competition from the individual description with a FON around the central position, to the way of assuming *competition effect* on growth with the C calculation, then the problem is only of semantics. In this case, I understand why for them, then yes the “FON approach” is creating asymmetric competition. I do not consider the “FON approach” as all that because I used a different way of transforming the FON integration into a *competition effect* in the IBU model, and even changing the “sharing tolerance” in my KiWi studies (Chapter 4). Would the original authors of the “FON approach” call

the use of the FON in IBU something different than a “FON approach”?

Chapter 9

General Discussion and Conclusions



9.1 Organization of this chapter

In this last chapter, I should come back to the specific advances given by each part to the field of mangrove ecology and the respective topics: (1) mangrove forest dynamics and (2) *Ucides cordatus* biology. I shall cover these topics in the two first sections, focusing also on answering the specific objectives of each part given in the general introduction (pages 18 and 20 respectively). I discuss in a third section the contributions of the thesis to the specific fields of individual-based and pattern-oriented modeling. In this same section I discuss also the pattern-oriented modeling information criterion (*POMIC*) to answer the methodological objective given in the introduction (page 16). In the last section I present general conclusions analyzing the possible parallels between the two focus systems and their respective levels of competition. This should allow an evaluation of the thesis' contributions to the general objective (given page 15). In this fourth section I finish proposing an idea of theoretical framework for complex representation of individual-based interactions.

9.2 Discussion on Part I. Interspecific competition in Caribbean mangrove forests

9.2.1 General contributions to mangrove forest ecology

The field work and modeling of mangrove forest structure and dynamics increased the knowledge on factors potentially influencing species zonation patterns by proposing a new factor: the perturbation regime. Although always considered as a factor influencing forest structure (e.g. Smith and Duke 1987), the perturbation regime was never linked to specific effects on zonation patterns until 2006 with the publication of Chapter 3 and in parallel the work of Imai et al. (2006), which proposes a very similar aspect. Chapter 4 illustrates that mangrove stand diversity could be directly influenced by perturbation regimes. When considering that a zone in nature could be a stand simulated in this study, this confirms the findings on species zonation: the heterogeneity of the zones of a site can be dependent on its perturbation regime. Chapter 5 proposes to organize the hypotheses influencing species zonation depending on the scale of action and the capacity of each factor to create or influence the patterns (particularly with Fig. 5.1). Chapter 5 re-demonstrated the importance of abiotic gradients on the installation of species zonation patterns in Calabash Cay as hypothesized by the statistical

analyses of Chapter 3. This was concordant with the hypothesis of species adaptation to abiotic gradients proposed by Macnae (1968) and Rabinowitz (1978) and analyzed at different scales by other authors (e.g. McKee 1995, Feller et al. 2002).

Chapter 4 also improved mangrove forest ecology knowledge on the question of application of the intermediate disturbance hypothesis (Connell 1978). This was, to my knowledge, never shown before for mangrove forests. Chapter 4 concludes on the importance of the local configuration of species interaction that itself depends on abiotic conditions and dynamical phase (temporal sequence of a succession phenomenon) to evaluate what could become the effect of a perturbation. The findings of Chapter 4 also propose a closer look toward succession of mangrove forests through the observation of species diversity patterns related to past perturbation regimes.

9.2.2 About interspecific competition

Zonation of species along the intertidal can be seen as a capacity of the species to partition the habitat and thereby resources: each species should be dominating the areas where they have their most favorable conditions. The work on the abiotic settings influencing zonation (Chapter 5), showed that factors influencing only growth and not establishment (salinity and nutrient availability in the simulation settings) had higher importance on the appearance of zonation patterns of sites with relatively mix species dominance (high index of species dominance heterogeneity). The factors influencing establishment (tidal sorting or seed availability) were complementary to these first factors on the sites with clearly defined zones. The factors influencing only growth could be seen as a set of factors linked to resource partitioning through the different growth strategies of the species in given environments. The second factors (i.e. influencing establishment) could be seen as factors related to the capacities of the species to partition their resources through different reproduction and establishment strategies. Interspecific competition might have been at the origin of evolution and adaptation of all these strategies (growth, reproduction and establishment) leading to habitat partitioning, but this would require demonstration, and is so far purely speculative. The influence of interspecific competition in this differentiation of realized niche of the three Caribbean species is particularly speculative considering that they are not a monophylogenetic group, with probable different origin of speciations (Saenger 2002). The actual spatial interspecific competition that we simulated through the use of the FON approach with species-specific settings was not seen as enough to reproduce the zonation patterns of Calabash Cay. Therefore, spatial interspecific competition does not appear to be a major

factor for the spatial organization of these three Caribbean species in zones across the intertidal.

The succession of species dominance was indirectly studied with the creation of different scenarios with different FON settings (Chapter 4). Both a fast succession (less than 50yr) and slow variation of overall dominance (over 500yr) were observed depending on these FON settings. The FON setting based on identical spatial competition strength of the three species did not show succession, but followed the original senescence phases seen in the first mangrove IBM simulator (Chen and Twilley 1998). The possibility of senescence phases in Caribbean mangrove forests is highly questionable because of permanent perturbations of these ecosystems with storms of different sizes (see also General introduction, section 1.3.2, page 12). The other FON setting, based on species-specific strengths, produces the fast succession pattern. We saw that this succession pattern has an important influence on producing an intermediate disturbance hypothesis pattern. But additionally, the resulting fast succession is corroborated with field observations of Ball (1980) in Florida and Berger et al. (2006) with the same group of species in Brazil. Species-specific spatial competition strength might therefore be likely to happen in the Caribbean mangrove tree community. We did not test directly if other factors could influence the reproduction of succession. However, the change of dynamics with the change of competition setting might lead to believe that interspecific competition is a major factor for the succession in tree species dominance in Caribbean mangroves.

9.2.3 Outlook

Overall, the three studies showed the importance of species-specific characteristics to cope with physical-chemical environment (in a broad sense) in order to create zonation or other types of habitat partitioning. The work on the influence of perturbation regimes (Chapter 3 and 4) showed that species recovery was profoundly dependent on the individuals left after a disturbance. Several work already analyzed the different responses of mangrove trees to destruction by strong winds depending on their species or sizes (e.g. Vermeer 1963, Stoddart 1963, Bardsley 1984, Roth 1992, Smith et al. 1994, Roth 1997, Imbert et al. 1998, Sherman and Fahey 2001, Baldwin et al. 2001, Imbert 2002). I did not incorporate these observations on the simulation exercises because of their lack of consistency throughout the Caribbean. However, following the recovery of a specific site, these observations could be incorporated in simulations and would probably lead to other interesting findings on questions of species dominance depending on the strength of the perturbation.

The three studies also illustrate the importance of forest dynamics on the understanding of forest structure. These works are the continuation of dynamical assessment of forest structure with theoretical models (e.g. Jiménez et al. 1985, Duke 2001, Fromard et al. 1998, 2004) or simulation models (FORMAN, Chen and Twilley 1998, KiWi, Berger and Hildenbrandt 2000). Simulations studies should be performed in these directions to understand further on the influence of abiotic settings, biotic interactions and external perturbations on species zonation patterns. Generally, other simulation exercises with more numerous patterns to reproduce, and multi-scale models, could help in answering the importance of each proposed factors on the installation and changes of species and structural zonation patterns in mangrove forests. Ultimately, considering the species zonation patterns, these further simulation studies could help in answering the general hypothesis observed in other intertidal areas: interspecific competition is an important factor in driving species spatial distribution across the intertidal (e.g. for review on evidence of competition in shaping rocky shores benthic communities, see Nybakken 2001 p253-255).

9.3 Discussion on Part II. Intraspecific competition in North Brazilian *Ucides cordatus* populations

9.3.1 General contributions to intraspecific competition among *Ucides cordatus*

The field work on *Ucides cordatus* (Chapter 6) documented the spatial distribution of this species in a North Brazilian mangrove, and proposed the hypothesis that these patterns of distribution are influenced by competition for resource at small scale (<10m) while more driven by habitat type at large scale (>10m). Chapter 6 showed a clear preference of *U. cordatus* individuals to be close to *Rhizophora mangle* roots and more generally under *R. mangle* trees. These findings confirmed indirectly the observations of Nordhaus (2004) that *R. mangle* leaves are the preferred food of *U. cordatus*. The small scale findings once integrated in the IBU model confirmed the hypothesis that intraspecific competition at individual level is an important factor for the organization of the population on a small scale (Chapter 8).

Chapter 8 also showed that random reason for movement of crabs might lead to recovery of harvested areas with equal evidence than with an intraspecific competition-based reason for movement. This could be seen as

contradicting findings of Chapter 7 at first, but several factors should be taken into consideration. The patterns used on Chapter 7 focused on the reproduction of the recovery of harvested area with a linear recovery, while Chapter 8 used the raw data points as pattern. Both the linear and the raw data patterns are interesting to reproduce, the first for probable underlying processes leading to this observation, and the second for the higher reliability on the points of observations (since the first is a statistical model of the second). Chapter 8 focused on the second aspect using the *POMIC* approach. Chapter 7 was focusing on frequency of movement questions. It showed that for the linear pattern to be reproduced, the random movement model needed an unrealistically high frequency of movement. This was reduced when using the competition model and linearity was then more easily reproduced. Chapter 8 complemented on this aspect showing that even if not considering the linearity, the model using random reason for movement still have a lower goodness of fit than models using competition as reason for movement. The use of the *POMIC* allowed then to identify that these two types of models had similar evidence, an assessment not entirely possible with mean-square deviation or root-mean-square deviation measurements as in Chapter 7. But generally, Chapter 8 complements the findings of Chapter 7 that spatial competition is triggering the movements of individual crabs.

9.3.2 Discussing further implications of intraspecific competition on *Ucides cordatus* population

The findings on movements of crabs being dependent on intraspecific competition and thus on density were discussed in Chapter 7 in term of necessity to protect the buffer areas that constitute non-fished areas under *R. mangle* roots. Particularly, considering that the spatial distribution pattern at small scale was seen as the results of competition among individuals, movements of *U. cordatus* were verified to be density-driven. Chapter 7 proposes to be particularly cautious on the techniques of harvest that crab collectors might use to catch *U. cordatus* under the *R. mangle* roots. The role as temporally slower buffer of secondary areas, such as forests of the Caeté peninsula dominated by other tree species, were also discussed on Chapter 7. The results of Chapter 7 and the knowledge acquired on Chapter 6 (and Diele 2000) showing that *U. cordatus* individuals are smaller and more numerous in general on these areas, could propose a multiple-scale buffer system (temporally and spatially). In this system, small individuals would grow on peripheral habitats and, while growing, move toward preferred habitats, namely under *R. mangle* trees. Since the areas around these trees are being harvested by

humans, the growing crabs would basically be coming closer and closer to the fishing ground of crab collectors until finally be caught.

Chapter 8 could not conclude definitively on the importance of asymmetric competition among individuals of different sizes for their decision to leave an area. Thus, I cannot verify the hypothesis of large scale population organization driven by asymmetric intraspecific competition for the best habitats. If the asymmetric competition is verified with future work, it could have implications for the ideas of multiple-scale buffer. The first implication would be the explanation given above of spatial organization by out-competition and therefore exclusion of small crabs from the preferred habitats of *U. cordatus* on *R. mangrove* forests. Some works of Diele (personal communications, manuscripts in preparations) would argue in favor of the establishment of very small individuals (just after last metamorphosis) close to large individuals. These small individuals could apparently grow their first year as crabs in coexistence with larger individuals due to feeding differences (Diele, personal communications). Asymmetric competition would start occurring once the small crabs begin to feed on *R. mangrove* leaves. These small individuals would then be excluded toward worse habitats. Once in these less favorable habitats, as the crabs grow, the hypothesis of multiple-scale buffer system assume that these individuals would come back step by step toward better habitat. However, asymmetric competition would hardly be an hypothesis explaining this movement back. In the worse habitats the crabs growing bigger would have no reason to leave these habitats, since they would collect easily all the available food against the smaller individuals. The habitat and food quality should have then a role on movements of growing crabs back to the preferred habitat. The role of competition might then be less important on this aspect of large scale buffer systems.

9.3.3 Outlook

Finally, other modeling studies including habitat quality could help on the analysis of the different scale buffer systems and on the presence and importance of asymmetric competition among crabs. The IBU model scale of integration (the individual) might become a problem for large spatial scale analyses because of computation limitation in dealing with a high number of individuals. However, upscaling methods exists (e.g. Jeltsch 1997) using the results of small scale models into models working at higher scale. Such an approach might be necessary to analyze the multiple-scale questions. Ultimately, the IBU and KiWi model could be used in parallel to simulate the effect of tree position on crab spatial distribution and to analyze multiple-scale buffer systems. These parallel models should then simulate growth rates and

competition strength of individual crabs depending on the spatial leaf-litter variation following tree growth and positions. It could eventually integrate a component of soil quality variation for trees depending on aeration by crab burrows. An interesting pattern-oriented modeling work would be to analyze if the presence of small crabs could explain patterns of tree re-growth and eventual reforestation seen in degraded area of the Caeté peninsula.

9.4 Discussion on ecological modeling

9.4.1 On individual-based modeling

The part on mangrove forest dynamics (Chapters 4 and 5) used an already established and recognized spatially-explicit individual-based model: the KiWi model (Berger and Hildenbrandt 2000). The second part presented and used a new spatially-explicit individual-based model: the IBU model (Chapter 7 and 8). Although the specific questions of focus were different, one simulating individual trees of different species focusing on their interspecific competition and the other simulating moving crabs and their intraspecific competition, these two parts took part in a process already started with many other theoretical works (e.g. Berger and Hildenbrandt 2003, Berger et al. 2002, 2004, 2006, Bauer et al. 2002, 2004): the generalization of the Field Of Neighborhood approach in analyzing spatially explicit competition situations.

Chapter 4 particularly innovated on applying the FON approach and an IBM to situations of perturbation regimes to analyze the possibility of occurrence of the intermediate disturbance hypothesis (IDH, Connell 1978). This setting of modeling analysis was innovating because spatial competition is of high importance in analyzing perturbation regime influence on species diversity, but was to my knowledge never integrated at the individual level for analyzing the IDH occurrence. Spatial processes are seen as more and more important in the explanation of diversity patterns (e.g. Tilman 1994, Pачepsky et al. 2001) and species coexistence (Barot and Gignoux 2004). Spatial competition at the individual level was seen as influencing species relative abundance distribution (Pачepsky et al. 2001), in accordance with the results of Chapter 4 on the importance of species capacities of spatial competition. Chapter 4 particularly confirmed the axioms of dependence of the reproduction of the IDH pattern detailed by Sheil and Burslem (2003): on succession occurrence, on succession due to competitive exclusion, and on perturbations bringing the system to earlier successional stages. This is a good example of hypothesis assessment with an individual-based (and more generally process-based) simulation model.

Chapter 7 and 8 presenting the IBU model innovated also on two aspects of individual-based modeling. The first one was to incorporate the spatial competition aspects of an animal during feeding phases and the interference competition produced by direct interaction with neighbors within a phenomenological competition model. As said on Chapter 7, this was previously done only with the GECKO model (Booth, 1997), although not mentioned as such. The integration of two different types of competition, generally analyzed separately in other animal IBMs, made the IBU model to reproduce three patterns of expression of competition. The second innovative aspect was to compare several individual-based approach of competition on Chapter 8. These comparisons brought understanding into asymmetric competition realization with individual-based approaches. They particularly proposed the FON as a solution to simulate real symmetric competition, hardly realizable with other approaches. In future works, these different approaches could be further investigated in term of behavioral interpretations, and compared to more mechanistic approaches of simulating resource use and competition.

The fact that the FON approach simulates phenomenologically the competition among individuals was seen as a drawback by a recent review on representation of competition for the study of self-thinning (Reynolds and Ford 2005). This critic is based on the need for self-thinning studies to understand the process of resource sharing among individuals leading to the specific biomass-density trajectories. At this level, considering trees growing in a stand without reproduction, it is true that the FON does not simulate mechanistically the resource use. However, the use of the FON approach in the KiWi model allows including an identical way of estimating spatial competition effect at all phases of the life-cycle of an individual: it includes competition during establishment, growth and ultimately determine the death of the individuals (through growth repression). In Chapter 4 and 5 the competition effect on growth also influenced indirectly the reproduction capacities of individuals. Thus, considering the life-cycle of an individual as the temporal basis of a community study (as in Chapters 4 and 5), the KiWi model using the FON approach is mechanistically simulating processes that can influence community structure.

The uses of the FON and other so-called “phenomenological approaches” with the IBU model also demonstrates that depending on the focus of the ecological question, the phenomenological aspect of a model is relative. The focus of IBU so far was not to reproduce the feeding and direct interactions of crabs, but to look at the potential general effect of spatial competition on decision for movement. The need of including both interference and exploitation competition led to a choice of phenomenological representation of competition. However, the overall behavior of the crab as opening/closing

its burrow, deciding to move, checking potential burrows for installation and installing were mechanistic. The analysis of the effect of this overall behavior on population structure might also be done phenomenologically with diffusion-process equations for the analysis of temporal patterns. However, this would never allow understanding the process behind the regular spatial organization at small scale.

As proposed above (section 9.3.3 page 231), IBMs to study mangrove ecology could be enhanced by multiple scale approaches eventually integrating IBU to KiWi. Although they were both developed in an object-oriented language (C++), this would be technically cumbersome because of the KiWi source codes incorporating many specialized algorithms to make it usable with a Visual Basic user interface. However, parallel runs of the two models could be a solution with outputs of one as inputs of the other. This realization would become a wider innovation into individual based modeling and the development of ecosystems representations with individual primary producers and individual primary consumers influencing each other and within each level, competing among them.

9.4.2 On pattern-oriented modeling

The pattern-oriented modeling approach (POM, Grimm et al. 1996, Wiegand et al. 2003, Grimm and Berger 2003, Grimm et al. 2005) was applied to develop the individual-based model IBU. We followed the 4 steps of the protocol (see General Introduction, section 1.1, page 5). 1) The biological knowledge accumulated on crab behavior during the MADAM project (specifically Nordhaus 2004 and Diele 2000) was integrated on this IBM. 2) The parameters of individual behavior were selected first according to estimates from population level data or behavioral estimations. The processes simulated were selected to focus on the reproduction of the recovery pattern, while still including realistic individual behavior. Obviously, the model complexity presented in Chapter 7 is the result of several trials and errors of development, selecting or not processes and parameter values to arrive to a good compromise between model complexity and payoff in pattern reproduction (what Grimm et al. (2005) present as the Medawar zone of a model). 3) The model results were systematically tested against the patterns of recovery and spatial distribution pattern. As secondary outcome (4), the asymmetric competition and distance of importance of resources were analyzed. This led to the proposition of new field work in order to document a pattern that could help inferring on asymmetric competition in a future POM cycle.

The same type of POM cycle is what made the KiWi more and more reliable as IBM to study the dynamics of Neotropical mangrove forests (from Berger and Hildenbrandt 2000 to Berger et al. 2006 and Chapters 4 and 5). Further, the POM approach allowed parameterizing another species of mangrove tree from the Indo-West Pacific (*Rhizophora apiculata*) for the KiWi model (Fontalvo-Herazo, in preparation). This should give precise-enough description of forest dynamics to use the model to assess silvicultural questions for the management of some IWP mangroves. As secondary outcome, the KiWi model in the present thesis produced succession and documented possible species dominance variations of the system depending on perturbation regimes. This was proposed in Chapter 4 as a basis for new field sampling to document species succession. Chapter 5 was the first POM procedure applied to KiWi using a quantifying indicator (*POMIC*) to analyze systematically the quality of reproduction of the patterns by the model results.

9.4.3 On the use of *POMIC*

The *POMIC* development was presented on Chapter 2 with a relatively simple example of application. The number of processes and parameters involved in this example are not corresponding to the level of complexity that traditional IBMs might present. However, Chapter 5 application of *POMIC* showed its use for more complex simulation model. And Chapter 8 application of *POMIC* in parallel to the mean square deviation demonstrated the capacity of the information criterion to infer on multi-pattern situation selecting models among a set of possible non-nested ones.

In this two applications, the complexity of the models was not considered as a criterion of selection. This was not in focus because the orientation of each study was to infer on possible processes (what is described as “strong inference” in Chapter 2) and not only to parameterize a best model to select for additional use. In the eventuality of willing to apply an “Ockham’s Razor” principle as described in Chapter 2 for the ultimate selection of a model within a set of models of identical evidence, we would need to describe and argue about the complexity of each proposed model. In the case of the KiWi study, this would have been relatively easy following the number of null sub-model (*TideO*, *HomogeneousNut* and *HomogeneousSal*) in each model result, assuming that a null sub-model is less complex than the others. Identically, in the IBU study the random sub-model of reason for movement could be considered as the least complex. The ranking of complexity of the other 3 sub-models would follow their respective mathematical complexity. It can be noted that this ultimate selection step taken as “the best model”

to make inference would have changed a bit the specific interpretation of the 2 studies, but not the general messages.

Later *POMIC* applications should focus on using it both for the inverse modeling steps and strong inference procedure. A statistical examination of the capacities of *POMIC* would also help it in becoming accepted to the “individual-based modelers” community. And particularly, a deeper comparison between this criterion and methods of model selection with multiple criterion using deviances methods (as in Wiegand et al. 2004 a,b) should be done.

9.5 Integrating the ecological lessons from Parts I & II

9.5.1 General conclusions

The understanding of the factors driving spatial distribution of species of high importance within an ecosystem is highly valuable for the understanding of spatial distribution and dynamics of other species. Particularly, the two components of the present thesis (mangrove trees and burrowing crabs) can be seen as engineering the shape of many spatially distributed resources in mangrove ecosystems. The canopy, the trunk, the roots, the shading, the leaf-litter or the propagules of trees are resources for many other organisms in mangrove ecosystems. The holes in the sediment, the excavated mud, the feces, or the burrowing crabs themselves are also resources for other organisms. *Ucides cordatus* in North-Brazilian mangroves is a very good example of these. The places to find these two key groups and the processes driving the distributions are therefore interesting for the understanding on other species spatial distributions and dynamics of Neotropical mangrove ecosystems.

Using identical individual-based modeling approaches, the two parts of the present thesis illustrate some interesting parallels and differences of processes influencing the spatial and temporal distribution of these two groups. The spatial patterns seen in the field were reproduced as properties emerging from the individuals’ intrinsic characteristics. However, the role of spatial competition in explaining these patterns was different. The interspecific competition for space was apparently not so important in explaining species zonation pattern of Caribbean mangrove trees. On the other hand, the intraspecific competition for space among *U. cordatus* was apparently driving small scale regular spacing of their burrows. The two spatial patterns of focus were of

different nature (one looking at species distribution, the other at individual distribution) but the levels of competition investigated were corresponding to these patterns (interspecific/intraspecific).

Competition among individual trees is believed to be at the origin of regular spacing after self-thinning phases of forests and was documented (e.g. Kenkel 1988). In this hypothesis, the death of individual trees that do not support the strong competition pressure of their neighbors would be at the origin of a regular spatial distribution of the remaining trees. The out-competition of individuals is similar to the process probably happening among crabs and leading to the observed spatial pattern at small scale. As such, the process of movement of these crabs because of competition could be compared to the process of death of sessile individuals under high competition pressure. Mobile organisms use mainly the movement as strategy to avoid or increase interaction, in particular predation, reproduction or competition. Sessile organisms under high competition situation do not have these abilities and have no other option than to die. This comparison is interesting in the sense of observing different strategies of organisms (go away, or compete to death) under an intraspecific competition situation leading to identical spatial patterns.

The succession patterns analyzed on the first part are also giving information that could be interesting for the second one. The first part showed that spatial competition might be at the origin of succession of species dominance. It could be considered that the crabs of different sizes have different spatial competition strength as the individual trees of different species. Thereby, the succession driven by competition could be investigated also for crab population dynamics. Particularly, if the asymmetric competition hypothesized among crabs of different sizes really occurs, the recovery of emptied area could be done first by small individuals later replaced by large ones. This, because the small crabs would, in case of asymmetric competition, be the one moving more often and thereby come back first to an emptied area. These size differences during the recolonization process should be documented with further field experiments. And the overall dominance per size-classes could be analyzed in parallel.

In general, further studies should go deeper on evaluating the role of spatial competition in influencing dynamics and spatial distribution in mangrove ecosystems. For example, a field study documenting the individual-level spatial distribution of trees within the ecotones of species dominance of a zonation pattern could give interesting patterns of aggregation or regularity of individuals of different species. Coupled with a pattern-oriented modeling

approach it would be possible to evaluate how to reproduce these patterns and thereby increase the reliability of estimating the role of interspecific spatial competition in the shaping of zonation patterns. Another example could be to look at how to reproduce the large scale distribution of *U. cordatus* showing a sort of zonation of crab sizes along elevation gradients of the intertidal (as documented in Chapter 6). This spatial distribution was seen as apparently driven by abiotic conditions. But the additional role of inter- and intra-specific competition on this distribution was not entirely investigated.

Finally, interactions between the two groups are also to be investigated. As said above (section 9.3.3 page 231, and section 9.4.1 page 234), multi-level models would help for these analyses. Individual-level information on effect of burrowing activities to the physiology of mangrove trees would be necessary. Lots of works are therefore still remaining on these two areas (modeling and field work). And ultimately, this could help to answer the questions proposed in Chapter 6 and partially above (section 9.3.3 page 231), as to know which of the two ecosystem engineers, the trees or the burrowing crabs, is first to recolonize in gap areas, and whether specifically *U. cordatus* influences the patterns of vegetation zonation in Brazil as proposed for grapsid crabs in Indo-Pacific mangroves (Smith 1987).

9.5.2 Concluding on inter- and intra-specific competitions

As seen above, the effects of inter- and intra-specific competition on community or population structures can be paralleled when considering patterns of respective interests. The general theories developed from questions of co-existence at ecosystem level can be used at the simpler community level (e.g. the IDH in Chapter 4) or even population level (e.g. implication of asymmetric competition on succession that might occur with different sized crabs during a recovery). Reversely and more importantly, the understanding of how competition works and what patterns are driven by the interactions at the population level (e.g. self-thinning, regular spacing) can be useful for higher integration level understandings. An example in the present thesis is the species-specific parameterization of the FON approach with self-thinning patterns of monospecific stands. This information on how individuals interact at intraspecific level is transferred to the interspecific level.

The use of individual-based modeling can help a lot in the gathering of understanding of different levels of integration. This is obviously not new to IBMs, and either to the present thesis. But IBMs simulate, with different phenomenological degrees, the important processes happening for a common

unit of all ecological integration levels: the individual. IBMs are thereby looking at the processes emerging on each level of integration above the individual. Doing so, the roles of inter- and intra-specific competition are much easier to analyze. Eventually, IBMs could be used to look at the original question that created the separation among inter and intra-specific competition: how much is driven by each type in stable state condition (in Keddy 2001). However, IBMs, and particularly spatially-explicit ones, are used in other directions to understand the role of competition in the processes that shape communities. For example, Kerr et al. (2002) analyzed the coexistence of 3 different bacteria types depending on the starting density of each. They used laboratory work and an IBM for simulating the mechanical processes of competition to understand how and when coexistence can occur. Identically, many spatially explicit IBMs simulating theoretical species were developed with lattice-based evaluation of individuals' interactions to estimate the relative importance of interspecific competition and other factors in explaining species diversity (e.g. Pachepsky et al. 2001, Chave et al. 2002). A main contribution of the FON approach in analyzing species diversity patterns is that the strength of competition of individuals is following not only the species' characteristics but also and primarily those of the individual (i.e. size and growth rate influenced by abiotic condition at the individual's location).

To conclude on these aspects, the more realistic representations of spatial competition given by the FON or other individual-based phenomenological approaches used in the present thesis should become very useful to study interspecific competition in the future. Future work analyzing the role of spatial competition would particularly benefit from the integration of knowledge from different types of competition occurring in a community (inter-/intra-specific, but also exploitation/interference and asymmetric/symmetric). For example it would be very interesting to apply these approaches to other zonation patterns of intertidal areas renowned as influenced by inter and intra-specific competition: Rocky shores and, particularly, mussel beds that show evidence of self-thinning (Guiñez and Castilla 1999), intermediate-disturbance hypothesis examples (Lenz et al. 2004), and species zonation from interspecific competition (Nybakken 2001).

9.5.3 Proposition of a probabilistic approach

This last sub-section is an idea I have not tested yet. It came out of the considerations for representing spatial competition at the individual-level analyzed in the present thesis, and more particularly with Chapter 8. Thereby, I propose to the interested reader, to look at speculative aspects of what could

become complex individual-based modeling of natural communities simulating several types of interaction among individuals.

When an interaction among two individuals occurs through the need of a common limited resource, this interaction can be called competition. However, interactions might also be positive, and mediated among individuals because of a common resource or because one is resource of the other (c.f. General introduction, section 1.2, page 5, and Table 1.1).

When phenomenological approaches such as the fixed radius neighborhood (FRN, Pacala and Silander 1985) or the field of neighborhood (FON, Berger and Hildenbrandt 2000) are used to simulate competition, these approaches focus on the effects of interactions among individuals using spatially distributed resources or ultimately needing space as resource.

The FON mathematical structure, and the equivalent ZOI and FRN model of Chapter 8, are calculating only a sum of neighboring interactions over the individual's interaction area (in their respective F_A , $\sum Ov$ and N). This has been so far considered as competition, and is then transformed into competition intensity in all models. However, if the interaction among two individuals is mediated through a spatially distributed resource and leading to positive effects for them, the interaction sum could be transformed mathematically into a positive effect for the individual. This would then simulate facilitation. Eventually, if the interspecific situation is considered whereby one should get a positive effect but the other would not be changed by the interaction, the mathematical sum of interaction could be transformed into a positive effect for the first and not considered for the second. This would simulate commensalism. Considering these, one could see a first important potential of these phenomenological models to simulate all kinds of interaction within a community.

The mathematical sum of interaction described above, and specifically for the FON approach, could also be viewed as a sum of probability of interaction. In other word, considering a focus individual, the intensity of the field of neighborhood across its interaction area could be interpreted as its probability to interact with a neighbor at each specific point of the interaction area while trying to get (or produce) a resource. The figure 9.1 illustrates this proposition. The sum of these probabilities of interaction over the overlap area with a neighbor (F_A , as in traditional FON) divided by the total interaction area (A_{int}) would still be a probability of interaction with the neighbor:

$$P_{interaction} = \frac{F_A}{A_{int}}$$

This $P_{interaction}$ would be then the mean probability of interaction (over the area) with the neighbor. In an individual-based model assuming these aspects, this probability of interaction would be per time step. If all the $P_{interaction}$ with all the neighbors having an overlap with the focus individual's interaction area are summed, this sum would become quickly >1 and would not make sense in term of probabilities when crowded situation are simulated. However, this sum could be considered as total interaction intensity which would then be transmitted to a positive or negative effect to one of the individual's strategy. Note that in practice, this is exactly what the FON approach is doing in Chapter 8.

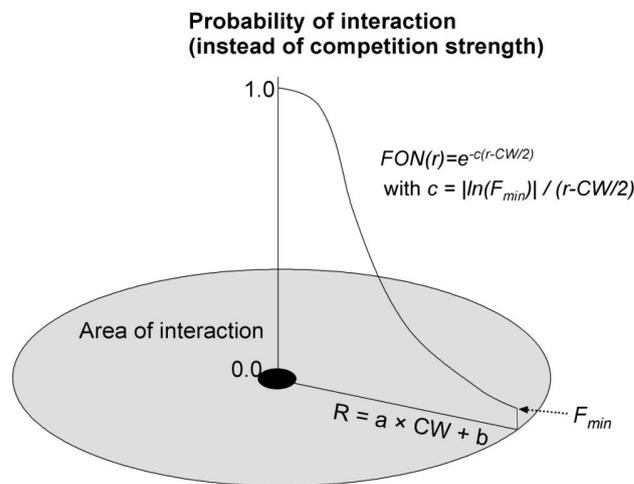


Figure 9.1: Change of interpretation of the field of neighborhood. The notion of the FON is considering a crab of carapace width CW , as in Chapter 8

However, this difference of interpretation of the FON makes things more interesting. First, the interaction would be in term of probability to interact for *one* resource. This would mean that the approach would become much more mechanistic, and one could then imagine having multiple FONs for different resources (proposed by Uta Berger). Secondly, the other phenomenological models used in Chapter 8 could also be interpreted in term of probabilities of interaction (Fig. 9.2). And this interpretation would give the possibility to use different shapes of interaction probability for different species according to their spatial resource use or creation efficiency. Other shapes could be thought of, as long as the mathematical integration of the sum of probabilities of interaction makes the model still runnable (e.g. Fig. 9.3). For example, for trees, this shape of probability of interaction for getting the light, could follow the traditional FON shape with a higher probability (1 at stem position) to get light close to the stem than going away. This

interpretation could even help for the parameterization of the approach since physiological characteristics of individuals would be considered. The traditional ZOI approach transformed into the phenomenological one presented in Chapter 8, could be representing the interaction probability of a territorial animal protecting its spatial “property” with a probability of interaction of 1 over the entire area.

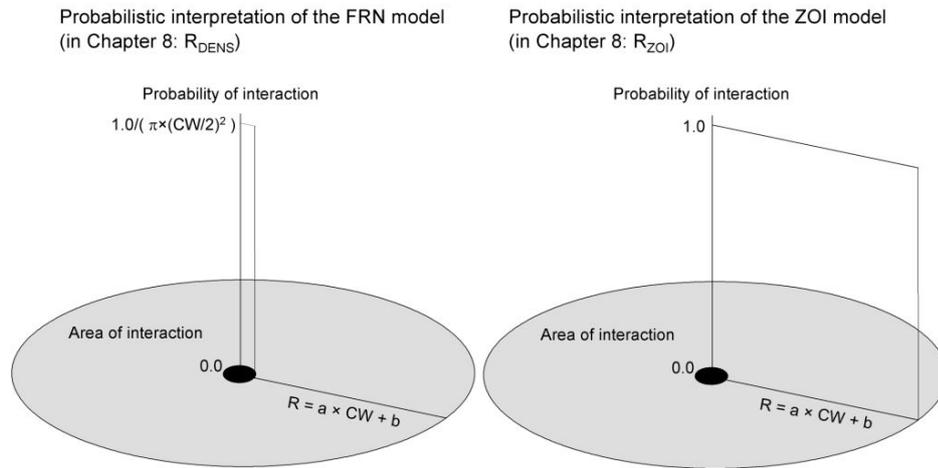


Figure 9.2: Different probabilistic interpretation of other phenomenological individual-based spatial models: the FRN and ZOI used in Chapter 8

Speculating further, with multiple FONs of different shapes for different resources and for different species, one could imagine representing a high range of possible systems with an IBM. For example, the mangrove tree community of focus in Part I could have three resource-based interactions: light, temperature and nutrients. The canopy shapes of each species would determine the type of radius calculation and probability of interaction to catch the light. The root system would be harder to parameterize but could follow another FON shape. And the temperature-based interaction could be the probability of facilitating establishment of seedlings limited by low temperatures (Fig. 9.3).

One could think of this general approach as a solution to look at many questions of coexistence or speciation. It would be very useful to evaluate the importance of different processes influencing individual success in a community, and thereby how species' strategies are favored. In the case of mangrove ecosystems, this approach could be very useful for the construction of multi-level models as proposed above, or further studies on specific aspects of dynamics of *Ucides cordatus* population or mangrove forest communities. However, this approach would have one strong drawback: the need

of simulating resource changes created by the individuals, which can become very complex when resources are not constantly renewed or spatially homogeneous. Finally, the *POMIC* and other “Ockham’s Razor” principles might avoid to use these complex models for prediction purpose as long as we do not have more patterns documented on systems of focus.

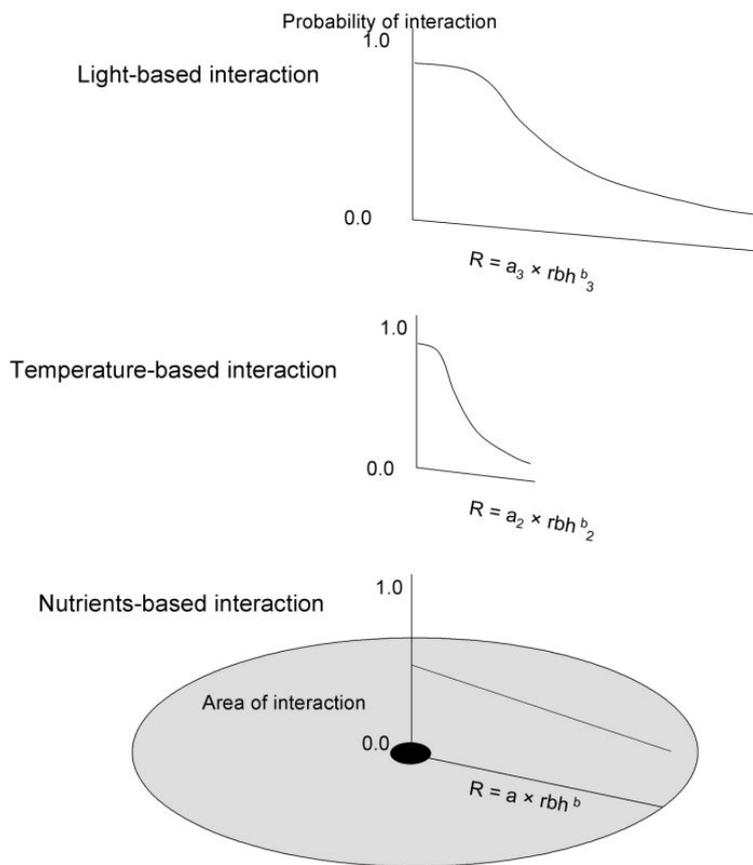


Figure 9.3: A proposition of probabilistic individual-based spatial representation of tree-tree interactions: light and nutrients are competed for, temperature-based could be a positive resource-based interaction

9.6 References

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