

IMPACT OF ANTHROPOGENIC DISTURBANCE ON A MANGROVE FOREST ASSESSED BY A 1D CELLULAR AUTOMATON MODEL USING LOTKA–VOLTERRA-TYPE COMPETITION

P.T. OBADE^{1,2}, N. KOEDAM¹, K. SOETAERT³, G. NEUKERMANS¹, J. BOGAERT⁴, E. NYSSSEN⁵, F. VAN NEDERVELDE⁶, U. BERGER⁷ & F. DAHDOUH-GUEBAS^{1,6}

¹Biocomplexity Research Focus, Laboratory of General Botany and Nature Management, Mangrove Management Group, Faculteit Wetenschappen en Bio-ingenieurswetenschappen, Vrije Universiteit Brussel (VUB), Belgium.

²Kenya Marine and Fisheries Research Institute, Kenya.

³Nederlands Instituut voor Oecologisch Onderzoek, Centrum voor Estuariene en Mariene Ecologie (NIOO-CEMO), The Netherlands.

⁴Laboratoire d'Ecologie du Paysage et Systèmes de Production Végétale, Faculté des Sciences, Université Libre de Bruxelles (ULB), Belgium.

⁵Image Processing and Machine Vision Group, Department of Electronics and Informatics, VUB, Belgium.

⁶Complexité et Dynamique des Systèmes Tropicaux, Département de Biologie des Organismes, Faculté des Sciences, ULB, Belgium.

⁷Department of Forest Biometry and Systems Analysis, Institute of Forest Growth and Forest Computer Sciences, Technische Universität Dresden, Germany.

ABSTRACT

Mangrove forests are ecologically and economically important and frequently dominating protected coastal areas in the tropics and subtropics at suitable intertidal zones and are often subjected to disturbances that disrupt the structure of an ecosystem, that change resource availability and that create patterns in vegetation by producing a mosaic of seral stages that ecologists have long recognised as important to landscape-level patch mosaics. Several good reasons justify the need for pursuing a predictive understanding of the ecology of mangrove species competition including the role of disturbance events and the aftermath. A predictive understanding can challenge our assumptions concerning the factors that control plant distribution and abundance and provide techniques for predicting rates of species change ranges in response to disturbances. The aim of this study was to evaluate and predict the impact of canopy disturbances on Gazi Bay mangrove forests and the subsequent vegetation patterns both spatially and temporally. The use of a simple 1D cellular automaton provided a detailed and nearly comprehensive parameterisation of the model by forest structure parameters belonging to the standard measurements of mangrove field surveys. In the study presented, the field data were obtained for disturbance impacts at various spatial scales considering not only the spatial extent of the disturbance but also its particular location. For this, multiple sampling transects were selected *a priori*, based on the vegetation patterns observed on Quickbird satellite image (2002) of Gazi, to reflect major ecological zones and vegetation transitions in space. Earlier field studies already revealed different population trajectories in some cases for the same pairwise species interactions, which are consistent with the hypothesis that different scales of disturbances may affect succession trends. Simulation experiments supported these findings by demonstrating that varying disturbance impacts determine coexistence or mutual exclusion of the interacting species and occasionally leading to equilibrium shifts to alternative states. We suggest the consideration of simulation experiments as a good proxy for predicting mangrove species dynamics not neglecting the need of further evaluation based on the transient ecodynamics. *Keywords: forecasting, Gazi, Kenya, mangrove, succession trajectory, vegetation dynamics.*

1 INTRODUCTION

Marine coastal ecosystems, of which mangrove forests are a part, are among the most productive and diverse systems on earth [1–2] and are of global importance to climate, nutrient budgets and often primary productivity [3–4]. Mangrove forests are ecologically and economically important often dominating protected coastal areas in the tropics and subtropics preferring suitable intertidal zones. Mangrove ecosystems, besides providing habitats for a wide range of marine

and terrestrial species [5–7], are a source of food, medicines and forestry products [8]. The tourism and recreational value of mangrove ecosystems is significant, and if this value is realised then it can contribute significantly to financing their management for local communities. A recent review of the major goods, services and functions of mangrove ecosystems is given by Walters *et al.* [8]. One important indirect value for the entire coastal zone is the protective function of coastal ecosystems against wave and storm energy, both in terms of ongoing coastal erosion and from potentially destructive natural disasters such as typhoons [9–11]. However, decision makers often undervalue these shoreline protection services [12] and the effects can be devastating, as evidenced by natural disasters such as the Indian Ocean tsunami (2004), hurricane Katerina (2005) and cyclone Nargis (2008). Though economic valuation of ecosystems needs to be treated with caution, the annual values per km² for mangroves are estimated to be US\$ 200,000–900,000 and are considered among the most valuable ecosystems in terms of their benefits to humankind [13]. Industrial activity, population growth, human migration to coastal areas, unregulated aquaculture development and poor management practices stress coastal resources, including mangrove systems [14–19]. Uncontrolled harvesting, destruction and even subtle changes in species composition of mangrove forests such as cryptic ecological degradation can permanently alter these ecosystems [10, 20]. Past studies indicate that it takes centuries for mangroves to recover from relatively minor disturbances [21].

The constituent plants of the mangrove community interact with one another, many a time in specific ways. The interactions are neither well studied nor understood. Importance is being attached to plant–plant interactions within the mangrove community because it is widely realised that the distribution and success of the mangroves cannot be adequately explained unilaterally on the basis of their interaction with the physico-chemical environment. Several categories of plant–plant interactions are argued to be important in determining the structure and/or function of the mangrove community, namely parasitic, antagonistic, mutualistic and competitive [22]. The aftermath of progressive biodiversity declines is dependent on the functional roles of individual species and the order in which species are lost [23]. Despite rapid changes in biodiversity in marine ecosystems occurring globally, the ecological impacts are poorly understood [2, 24].

A disturbance is a relatively discrete event that disrupts the structure of an ecosystem, community or population and changes resource availability or the physical environment [25]. Disturbances create patterns in vegetation by producing a mosaic of seral stages that ecologists have long recognised as important to landscape-level patch mosaics [21, 26–28]. The effects due to physical disturbances, depending on their nature, magnitude and other associated properties including the response, recovery ability and regeneration period of the mangrove species, affect mangrove biodiversity and evolution. Disturbance includes the factors that are involved in the destruction of plant tissue, such as the activities of herbivores, anthropogenic interventions, phenomena such as wind, hurricanes, sea level rise, tsunamis, El Niño–Southern oscillation-associated events [29], fire and erosion among others [22]. Major research topics in landscape ecology have over the years focussed on the causes, patterns, dynamics and consequences of disturbances [28, 30–33]. Collins *et al.* [34] argued that disturbances may even be required for the maintenance of community structure and ecosystem function. Concurring, Scheffer *et al.* [35] suggested that disturbance is a natural component of ecosystems that promote diversity and forest renewal processes.

It is interesting to note that disturbances create and also respond to landscape patterns. Their consequences usually include creation of open spaces such as gaps in otherwise continuous forests and, in many instances, alter levels of resources such as light and nutrients. The disturbance effects

on biota often depend on the state of the system before it was disturbed. For instance, tree heights influence the effect of uprooting and stem snapping that occurs in a forest affected by a catastrophic wind [36]. The successional stage of a community as well as the phenology of its members, when it is disturbed, may control the availability of propagules that determine, in part, the composition of the post-disturbance community.

1.1 Ecological modelling

Several good reasons justify the need for pursuing a predictive understanding of the ecology of mangrove species competition, disturbance effects and by extension, invasions. The predictive understanding we seek with the present paper can (1) increase our ability to mitigate the negative economic and environmental impacts of invasions or cryptic ecological degradation [37], (2) challenge our assumptions concerning the factors that control plant distribution and abundance [38–41] and (3) provide techniques for predicting rates of species range changes in response to disturbances including climate change. Simulation modelling is widely recognised to be a powerful tool for understanding the complexity of biological systems and a useful means of inference on long-term dynamics, especially given the rarity of comprehensive long-term data on vegetation dynamics [42]. This argument counts particularly for mangrove forests, there endogenous and exogenous processes [43] may cause canopy turnover taking hundreds of years under natural conditions [21, 44]. So far, there are three individual-based mangrove simulators available: FORMAN, MANGRO and KiWi [45], which were successfully applied to enhance knowledge and forecasts successional patterns in Neotropical mangroves [44, 46]. All three models require detailed knowledge about species-specific life processes on tree level under varying environmental conditions (e.g. growth rates of trees depending on nutrient availability and neighbour competition). Their parameterisation and application to real-world situations presupposes not only structural forest data on stand level but also data related to local competition processes such as light availability [44], neighbouring tree constellations [47] and nutrient availability in the spatial resolution of single trees. Such data are hard to obtain for both logistical and financial reasons, and they are not available for the study site in consideration. However, stand structure measurements can be easily obtained providing a descriptive formulation of potential competition outcomes among trees (see description given below), and analyses of satellite images available for Gazi Bay provide *a priori* knowledge about chronosequences of vegetation cover. In order to take advantage from this valuable information, the cellular automata (CA) approach [48–50] was selected as an appropriate tool for this study. Coupled with the principles of the Lotka–Volterra competition model, the CA developed in this study incorporates both intra-specific and inter-specific competition and considers neighbour competition spatially explicitly. Criticisms leveled against Lotka–Volterra competition model include having too many sets of assumptions for specific competitive interactions and also for important biological reasons ranging from time delays to mechanisms [51, 52]. Nevertheless, the chosen approach appears to deal best with the available datasets.

The aim of this study was to develop an effective but suitable methodology to evaluate and predict the potential impact of disturbance on Gazi Bay mangrove forest and behavioural spatio-temporal patterns combining field-based data of the mangrove structural attributes and simulation experiments. The specific objectives are derivation of input values for model parameterisation; analysing the sensitivity of vegetation dynamics due to different magnitudes of disturbance impacts and evaluation of the impacts of disturbance on long-term succession trajectories.

2 MATERIALS AND METHODS

2.1 Description of the study area

Gazi Bay is located about 50km South of Mombasa (Fig. 1) and is drained by two seasonal rivers, Kidogweni to the North and Mkurumuji to the South. The Gazi Bay mangrove forests are described as degraded and have been undergoing a recovery process mainly attributed to human intervention [53, 54]. The Kenyan coastline experiences mixed semi-diurnal tides, which is expressed in two high tides for every 24 hours with a considerable variation in the tidal amplitude between successive tides [55]. The maximum tidal range is approximately 4 metres.

Following extensive overexploitation of the mangroves of Gazi over a long period, especially for industrial fuel wood and building poles, a pilot reforestation project to rehabilitate degraded mangrove areas, restock denuded mudflats and transform disturbed forests into uniform stands of higher productivity was launched in 1991 [53]. More than 200,000 trees comprising mainly of *Rhizophora mucronata* Lam., *Ceriops tagal* (Perr.), C.B. Robinson, *Avicennia marina* (Forssk.) Vierh. and *Sonneratia alba* Sm. had been planted as monocultures in 12.47 hectares by 1995 [53]. Growth and survival rates obtained after 3 years suggested that the performance of replanted mangroves depended on planting material type, elevation of the forests and the size of saplings during transplanting [57].

2.2 Forest structure description

2.2.1 Field methodology and silvometric calculations

We used the Point-Centred Quarter Method which is schematically illustrated in Fig. 2 [58–60]. Transects and sampling points were selected to reflect the major ecological zones and areas of vegetation transitions with transects being selected *a priori* based on the vegetation patterns observed on the Quickbird satellite image (2002) of Gazi Bay [61]. The fieldwork data collection was designed to obtain the following data: (1) the structural attribute data that were used to calculate spatio-temporal values in the model to infer species interaction coefficients of mortality; (2) the basal areas that were used to parameterise the model and (3) other important parameters such as complexity index (*CI*), which gives an indication of structural development of a forest. In each assemblage, 20 sampling points were taken along a selected transect. GPS readings were taken using Garmin's GPS III. The tree heights were measured using a hypsometer. D_{130} , which is the tree stem diameter at 130 cm height along the trunk [62], is calculated from G_{130} (tree girth at 130cm) that was measured by tape, by dividing G_{130} by π .

The following parameters were determined [59, 60]: the stem density (*De*) and basal area (*Ba*) for each species, the mean stand height (\bar{h}) and the *CI* [63]. Blanco *et al.* [64] demonstrate comparative calculations and guidelines to compute *CI* in those mangroves where either seasonal or strong disturbances have occurred. *CI* is considered to be a reliable algorithm that represents spatial structure and development of forests by enclosing the current forest state, mean condition or steady state in a single value [64]. The relative density (DE_{ri}) is

$$DE_{ri} = \frac{100DE_i}{\sum_{i=1}^m DE_i}, \quad (1)$$

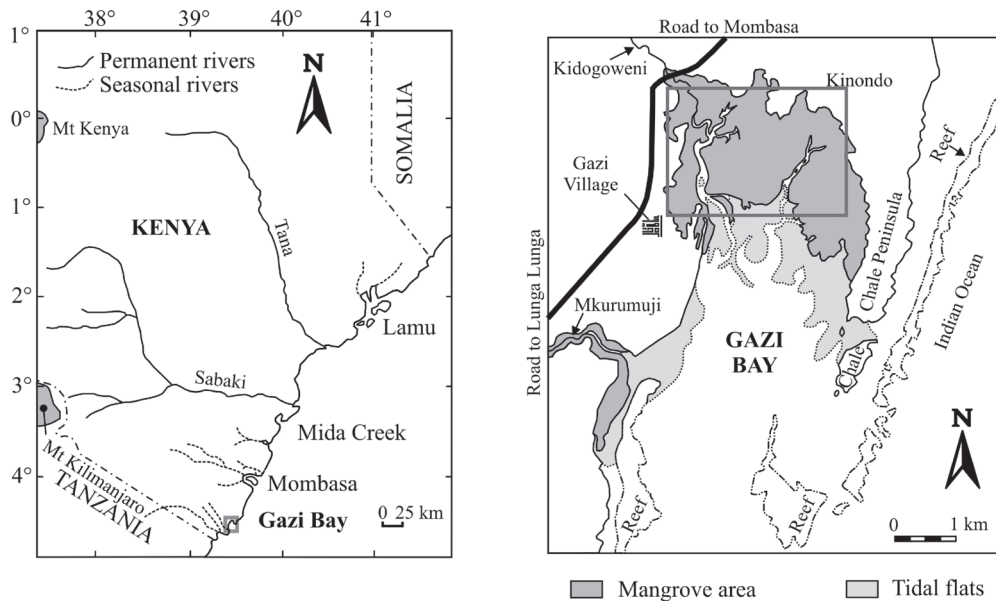


Figure 1: Map of Gazi Bay with an overview of the location of all the sampling transects (indicated by the rectangle) (modified from [56]).

where DE_i is the density for species i and m is the number of species. The relative dominance (DO_{ri}) is

$$DO_{ri} = \frac{100Ba_i}{Ba}, \quad (2)$$

where Ba_i is the basal area of all trees of species i . The relative frequency (F'_{ri}) is

$$F'_{ri} = \frac{100F_i}{\sum_{i=1}^m F_i}, \quad (3)$$

where F_i is the number of sampling points in which species i is represented 100 times.

The importance value IV [65] is calculated as

$$IV = DE_{ri} + DO_{ri} + F'_{ri}. \quad (4)$$

2.3 Modelling experiments

2.3.1 Model description

The model is implemented as a 1-D cellular automaton (CA). Each simulation experiment considers only two different species (i and j) which compete for (re-)colonizing empty cells. Trees, occupying neighbouring cells, also compete with each other for spatially limited resources. This process results in

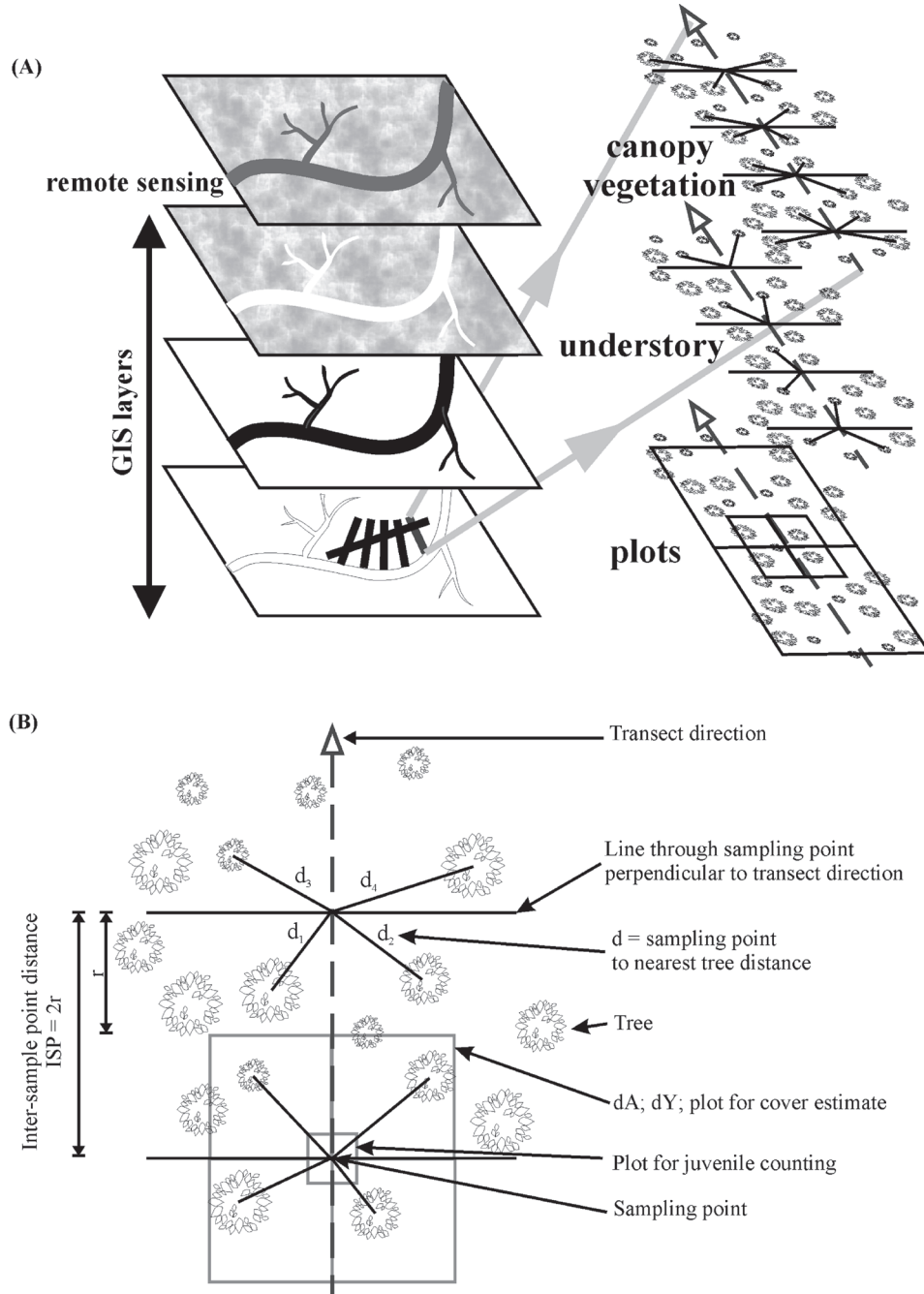


Figure 2: A simplified schematic representation of the Point-Centred Quarter Method (PCQM). (A) depicts the canopy cover layer which comprises mainly adult trees, while the understory comprises mainly young and juvenile trees. The distances to the nearest adult tree in each quadrat are represented by d_1, d_2, d_3 and d_4 as shown in (B).

the death of one of the involved trees and is described by a Lotka–Volterra sub-model basing on two coupled differential equations describing the population sizes N_1 and N_2 of the particular species [66]:

$$\frac{dN_1}{dt} = \frac{r_1 N_1}{K_1} (K_1 - N_1 - a_{12} N_2), \quad (5a)$$

$$\frac{dN_2}{dt} = \frac{r_2 N_2}{K_2} (K_2 - a_{21} N_1 - N_2), \quad (5b)$$

where r_1 and r_2 are the intrinsic growth rates; a_{12} and a_{21} are competition coefficients. The values K_{ij} refer to the carrying capacities of the species in a given cell (eqn (6a) and (6b)). These values are species specific, habitat sensitive and could – in principle – change over time due to species impact on environment, as well as other dynamic processes such as competition and predation [67]. The model, however, does not describe the latter.

$$K_1 = \frac{a_1 - \mu_1}{a_1} K = \frac{r_1}{a_1} K, \quad (6a)$$

$$K_2 = \frac{a_2 - \mu_2}{a_2} K = \frac{r_2}{a_2} K. \quad (6b)$$

The competition coefficients a_{12} and a_{21} are made up of more mechanistic parameters:

$$a_{12} = \frac{2\beta_{12}K + a_1}{a_1}, \quad (7a)$$

$$a_{21} = \frac{2\beta_{21}K + a_2}{a_2}, \quad (7b)$$

with a_i and a_j as species-specific reproduction rates and μ_i and μ_j as specific mortality rates. The model application is thus based on the following assumptions: (a) each species has a specific mortality which does not vary other time and is independent on the heterogeneity of abiotic factors; (b) β_{ij} and β_{ji} specify the competition factors – imposed on species i by species j and j by i particularly. Intra-specific competition is not explicitly considered but indirectly included in the specific mortality (μ); (c) each species has a probability to produce offspring a_i and a_j which can only be placed in empty cells remaining there until they die and (d) offspring are placed within species-specific distance from the parents' cell mimicking differences in their dispersal ranges [68, 69] (Fig. 3).

The competition factors (β_{ij} and β_{ji}) take into consideration both adult and young trees at species/ assemblage levels. They were described as spatio-temporal probabilities of occurrence of species (i or j) in a forest matrix dominated by another species (j or i). According to Curtis [65], this value is one-third the importance value of each species ($IV/3$), but divided by 100:

$$\beta_{ij} = \frac{IV_{ij}}{300}. \quad (8)$$

This coefficient expresses lumps major processes regulating the distribution and abundance of species in natural communities [67].

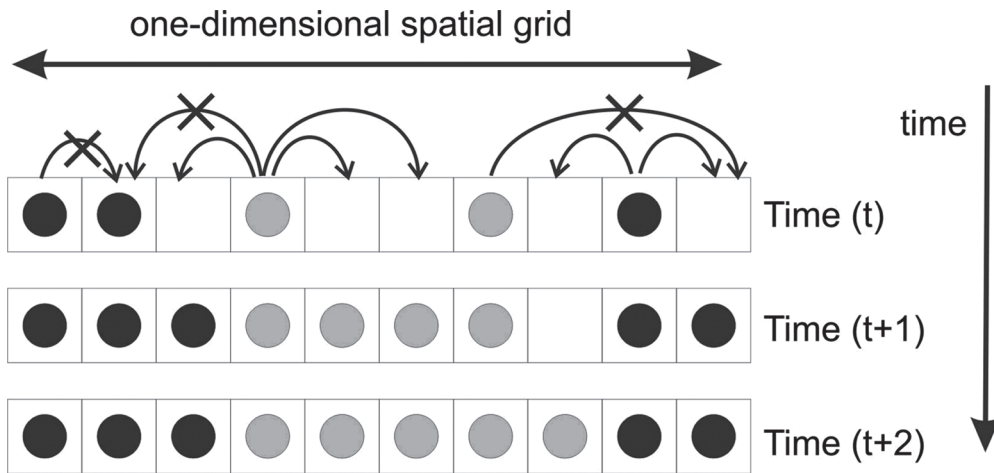


Figure 3: A simplified schematic representation to visualise dispersal assumptions and how competition generates the evolutionary patterns of the model simulations at different time steps (vertical axis downwards). Consideration is given to a 1-D array of grids for each time step. The black and grey circles represent two competing species with, in this hypothetical case, species 1 (black circles) having a dispersal range of 1, while species 2 (grey circles) having a dispersal range of 2. The curved arrows indicate which cells a certain species can or cannot occupy (not all possibilities are given). The ability of an individual to occupy the cells is based on the stipulated assumptions discussed in section 3.2.1 on the Lotka–Volterra model. In reality, an empty cell can be occupied by the first arriving species representative before competition begins. Once it settles, this individual cannot be removed until it dies.

2.3.2 Analytical analysis of the Lotka–Volterra sub-model

Equilibrium analysis of ecological systems described by differential equations is an important tool for analysing the systems behaviour and potential phase transitions and is widely documented in literature [28, 35, 66, 70–74]. In case of two coupled differential equations, a phase plane analysis is a well-known graphical tool for this purpose [75]. The analysis was carried out on all potential systems of two different tree species and for several plausible magnitudes of perturbations of the vegetation cover (10%, 50% and 90%, respectively) expressed by varying carrying capacities (K_1 and K_2) and interaction coefficients (a_{12} and a_{21}).

2.3.3 Grid size of the CA

The majority of CA models, describing plant communities or forests, use cell sizes which refer to the mean size of an adult plant or tree [76]. Taking this assumption in mind, the grid size for this study was estimated as mean available area for the trees:

$$\text{Grid size} = \frac{A_{st}}{SD} \text{ (units: m}^2\text{)} = 2.77, \tag{9}$$

where A_{st} is the stand area (0.1ha = 1000 m²) and \overline{SD} is the mean stem density (=361 trees). However, the unevenness of mangrove trees morphology and architecture introduces difficulties for using one specified grid size for all species at the same time. In order to avoid using different grid

sizes for diverse species interactions, the particular density of a species in a given grid cell was normalised by its basal area. The whole grid area was chosen to be 1000 grid cells during all simulations.

For example, the initial population values were determined by taking into consideration the carrying capacity values of the interacting species. In Gazi, changes in carrying capacity have not changed much in areas sampled, though this might still change in the future or with more fieldwork data. The remaining proportion was also taken into account and represented by empty cells. The proportionality of occupied cells or empty cells was assigned hypothetically in the ratio of 80% or 20%. Therefore, the proportion of cells occupied by pairwise interacting species for initialisation of species 1 and 2 was calculated as follows:

$$N_{ini(i)} = \frac{BA_i}{BA_i + BA_j} \times 0.8, \quad (10)$$

where $N_{ini(i)}$ is the initial population density proportion of grid cells for species 1; BA_i and BA_j are the basal areas of species i and j , respectively. At the end of each simulation run, the population density values of each species were re-converted to the number of trees in a particular stand by dividing its population density by the carrying capacity and multiplying this value by the stem density.

2.4 Disturbance analysis

A disturbance is a distinct event that modifies the structure of an ecosystem thus moderating the attainability of resources consequently affecting the landscape settings [25] and is therefore scientifically important due to its implications on the succession and zonation patterns of a system [36]. In the case of the mangrove forests of Gazi Bay, disturbances directly affect the vegetation cover of the mangrove forest. The question arises in which way the size and intensity of a particular disturbance event affects the resulting succession trajectory. For this, simulation experiments were carried out which start with a certain percentage of empty cells, mimicking the canopy disturbances, and the subsequent development of the vegetation coverage was registered depending on the available species during 600 simulation years.

2.4.1 Sensitivity analysis related to disturbances

In order to assess the influence of the magnitude of disturbances on the model outcome, simulation experiments were carried out for varying disturbances magnitudes described as 25%, 50%, 75% and 90% empty cells of all possible 1000 grid cells. The chosen magnitudes were selected according to the range of observed data [77, 78]. Based on the results of these sensitivity tests, the disturbance regime of the simulation experiments was determined as described below.

2.4.2 Simulation experiments related to canopy disturbances

The simulations were carried out for 20% and 60% of the simulated area. The 60% disturbance was not described as a compact area but sub-divided into three sections of 20% each. The locations of the disturbances were chosen according to the field observations: the landward and seaward edge areas are most likely to be disturbed by human intervention efforts such as anthropogenic-induced disturbance like waste water inflow or clear cutting. The latter is facilitated due to the easier accessibility by roads and channels and/or the proximity to human settlement areas. In addition, the seaward edges are threatened by natural disturbance phenomena such as erosion, accretion or sea level rise. For this reason, 20% of disturbances were always located at the edge of the simulated area.

Table 1: Relative density (DE_r), relative dominance (DO_r) and relative frequency (F_r) and spatio-temporal probabilities ($IV/3$) for major species in each species/vegetation assemblage calculated from the structural attribute field data.

	Species/vegetation assemblage														
	A.mar			B.gym			C.tag			R.muc					
	DE_r (%)	DO_r (%)	F_r (%)	DE_r (%)	DO_r (%)	F_r (%)	DE_r (%)	DO_r (%)	F_r (%)	DE_r (%)	DO_r (%)	F_r (%)			
A.mar	100.00	100.00	100.00	1.03	0.95	0.85	0.94	7.00	4.71	10.17	7.30	3.22	4.74	9.75	5.80
B.gym	1.22	0.88	1.23	64.94	62.42	51.52	59.62	0.63	2.49	3.64	2.25	5.22	17.78	9.40	10.80
C.tag	0.78	1.31	1.02	5.19	1.44	9.09	5.24	80.61	75.33	69.29	75.08	5.78	1.56	17.26	8.20
R.muc	1.04	0.96	0.89	29.87	36.14	39.39	35.13	11.77	17.47	16.89	15.38	83.75	70.02	62.30	72.02
S.alb	1.43	0.82	1.18	1.02	1.12	0.99	1.04	1.43	0.89	0.91	1.07	0.78	1.23	0.82	0.94

	Species/vegetation assemblage											
	S.alb			R.muc + A.mar			R.muc + C.tag					
	DE_r (%)	DO_r (%)	F_r (%)	DE_r (%)	DO_r (%)	F_r (%)	DE_r (%)	DO_r (%)	F_r (%)	DE_r (%)	DO_r (%)	F_r (%)
A.mar	0.87	0.82	0.96	0.88	51.71	37.01	40.04	6.41	28.55	11.63	15.53	
B.gym	0.95	1.12	0.81	0.96	1.20	0.92	0.89	1.00	17.95	28.71	25.58	24.08
C.tag	1.22	0.97	0.92	1.03	13.29	10.65	12.86	12.27	35.90	11.78	30.23	25.97
R.muc	4.08	0.34	9.09	4.50	54.62	33.25	48.61	45.49	39.74	30.96	32.56	34.42
S.alb	95.92	99.66	90.91	95.50	0.70	4.39	1.52	2.20	0.86	1.37	0.96	1.06

B.gym = *Bruguiera gymnorhiza*, C.tag = *Cerriops tagal*, A.mar = *Avicennia marina*, R.muc = *Rhizophora mucronata*, S.alb = *Sonneratia alba*, R.muc+A.mar = *Rhizophora mucronata/Avicennia marina*, R.muc+C.tag = *Rhizophora mucronata/Cerriops tagal*.

In the case of the 60% disturbance scenario, the second 20% of disturbances was located on the other edge of the simulated area whereas the remaining 20% were located in the innermost forest.

2.5 Model implementation

The model simulations were run 15 times for each pairwise interaction to statistically ascertain the variances of the population trajectory curves. The model was implemented in R-Statistics in the simulation environment Flexible Environment for Mathematically Modelling the Environment [79].

3 RESULTS

3.1 Forest structure description

Table 1 shows that the highest values of spatio-temporal probabilities of each species interactions were realised for species that occurred in their respective species/assemblage, for instance, *S. alba* in a *S. alba* stand registered 95.5% and *A. marina* in *A. marina* had 100%. The low values in particular stands give an indication that the likelihood of the species named in the rows to occur in these stands is rather low. The highest value of *CI* was 14.5 for *R. mucronata*, suggesting that it was best structurally developed mangrove forest at Gazi Bay. *R. mucronata* was the highest ranked according to the importance value of Curtis [65]. The rest of the rankings are *C. tagal*, *A. marina*, *Bruguiera gymnorrhiza* (L.) Lam. and *S. alba*. The basal area recorded for *R. mucronata* (2.51 m²/0.1ha) was the highest while that of *B. gymnorrhiza* (0.86 m²/ha) was the lowest.

3.2 Parameterisation of the model

The detailed analysis of the forest structure in Gazi Bay provided a full parameterisation of the competition factors β_{ij} and β_{ji} (Table 2). Other parameters such as the species-specific carrying capacities (*K*) of the grid cells and the dispersal ranges were estimated based on measurements of this studies; growth rates were available from studies previously carried out in Gazi Bay (Table 3). A few parameters (such as the mortality rates μ) had to be assumed as reasonable ones. The interaction factors *a* were calculated according to eqn 7 (Table 4).

Table 2: The interference competition coefficients β_{12} and β_{21} over an estimated 20-year period specify mortality imposed on species 1 by interactions with species 2 and vice versa.

	<i>A.mar</i>		<i>B.gym</i>		<i>C.tag</i>		<i>R.muc</i>		<i>S.alb</i>		<i>R.muc/A.mar</i>		<i>R.muc/C.tag</i>	
	β_{12}	β_{21}	β_{12}	β_{21}	β_{12}	β_{21}	β_{12}	β_{21}	β_{12}	β_{21}	β_{12}	β_{21}	β_{12}	β_{21}
<i>A.mar</i>	–	–	0.01	0.01	0.073	0.01	0.058	0.01	0.01	0.01	0.4	0.01	0.155	0.01
<i>B.gym</i>	0.01	0.01	–	–	0.023	0.052	0.108	0.351	0.01	0.01	0.01	0.01	0.241	0.01
<i>C.tag</i>	0.01	0.073	0.052	0.023	–	–	0.082	0.154	0.01	0.01	0.123	0.01	0.26	0.01
<i>R.muc</i>	0.01	0.058	0.351	0.108	0.154	0.082	–	–	0.045	0.01	0.455	0.01	0.344	0.01
<i>S.alb</i>	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.04	–	–	0.02	0.01	0.01	0.01

These values were inferred from the spatio-temporal probabilities as calculated from the PCQM data. Refer to Table 1 for species abbreviations.

Table 3: Parameters for the Lotka–Volterra sub-model which were used together with the β_{12} and β_{21} values in Table 2.

Species/assemblage	<i>A.mar</i>	<i>B.gym</i>	<i>C.tag</i>	<i>R.muc</i>	<i>S.alb</i>	<i>R.muc/A.mar</i>	<i>R.muc/C.tag</i>
Carrying capacity (K_i)	0.93	0.88	0.98	2.51	2.36	1.23	1.90
Dispersal range (D)	10	8	2	4	6	3*	7*
Growth rate/year (r_i)**	0.21	0.20	0.18	0.24	0.41	0.20*	0.20*
Reproduction rate (a_i ***)	0.26	0.25	0.23	0.29	0.46	0.25	0.25
Mortality rate (μ_i)	0.05*	0.05*	0.05*	0.05*	0.05*	0.05*	0.05*

Refer to Table 1 for species abbreviations.

*Represents assumed values.

**Represents data in Kairo [18].

***Represents values of reproductions rates calculated by the relationship $a_i = r_i + \mu_i$.

Table 4: The matrix values of the species interaction coefficients a_{12} (rows) and a_{21} (columns).

	<i>A.mar</i>	<i>B.gym</i>	<i>C.tag</i>	<i>R.muc</i>	<i>S.alb</i>
<i>A.mar</i>	0.000	1.080	1.584	1.464	1.080
<i>B.gym</i>	1.080	0.000	1.184	1.864	1.080
<i>C.tag</i>	1.080	1.416	0.000	1.656	1.080
<i>R.muc</i>	1.080	3.808	2.232	0.000	1.360
<i>S.alb</i>	1.080	1.080	1.080	1.080	0.000

The values of a_{12} (rows) and a_{21} for the main mangrove species/assemblages were estimated per 20 years and then converted to annual rates for input into the model. The calculation of these values is described in eqn (7).

3.3 Analytical analysis of the Lotka–Volterra sub-model

The changes in the competition interaction coefficients, a_{12} and a_{21} , does not affect the vegetation dynamics significantly for various degrees of perturbations. A 90% decrease in either a_{12} or a_{21} , however, results in pronounced species changes (Table 5).

This phenomenon is consistent for all pairwise interactions. However, when analysed further together with the carrying capacity values thereafter evaluating the coexistence inequalities [75], then it is apparent that some degrees of perturbations produce changes in equilibrial status. Due to lack of publishing space, we have opted not to show the actual phase planes but Table 5 gives a comprehensive summary of all the outcomes of the phase plane analyses and inequalities for the different perturbation scenarios for the permutations of interacting species. The values of reproduction rates (a) and mortality rates (μ) are incorporated as per eqns (6) and (7).

The pairwise interactions between *B. gymnorhiza* and *A. marina* (Table 5) depict an unstable equilibrium (according to the inequality scheme in Table 6) when there is no perturbation. However, for a 90% perturbation decrease, there is a stable equilibrium (Table 5) for the same pair at the end of the simulation. Despite the small variations for perturbations lower than 90%, the inequalities sometimes indicate change in equilibrial status when compared to pre-perturbation scenarios. For instance, in the interactions between *B. gymnorhiza* and *A. marina* at 10% perturbation decrease imply that *A. marina* will always be the superior species according to the coexistence rules described in Table 6, thus representing another equilibrial status for the same interactive pair.

Table 5: Displays summary outcomes at the end of selected pairwise simulations after being subjected to different levels of perturbations.

Species <i>i</i>	Species <i>j</i>	Effects of a_{12} and a_{21} perturbations						
		0	10% Increase	10% Decrease	50% Increase	50% Decrease	90% Increase	90% Decrease
<i>B.gym</i>	<i>A.mar</i>	U	U	Sp ₂	U	S	U	S
	<i>C.tag</i>	U	U	U	U	S	U	S
	<i>R.muc</i>	U	U	U	U	Sp ₂	U	S
	<i>S.alb</i>	Sp ₂	Sp ₂	Sp ₂	Sp ₂	Sp ₂	Sp ₂	S
<i>A.mar</i>	<i>B.gym</i>	U	U	Sp ₁	U	S	U	Sp ₂
	<i>C.tag</i>	U	U	Sp ₂	U	S	U	S
	<i>R.muc</i>	Sp ₂	Sp ₂	Sp ₂	Sp ₂	Sp ₂	Sp ₂	S
	<i>S.alb</i>	Sp ₂	Sp ₂	Sp ₂	Sp ₂	Sp ₂	Sp ₂	S
<i>C.tag</i>	<i>B.gym</i>	U	U	U	U	S	U	S
	<i>A.mar</i>	U	U	Sp ₁	U	S	U	S
	<i>R.muc</i>	Sp ₂	Sp ₂	Sp ₂	U	Sp ₂	Sp ₁	S
	<i>S.alb</i>	Sp ₂	Sp ₂	Sp ₂	Sp ₂	Sp ₂	Sp ₂	S
<i>R.muc</i>	<i>B.gym</i>	U	U	U	U	Sp ₁	U	S
	<i>A.mar</i>	Sp ₁	Sp ₁	Sp ₁	Sp ₁	S	Sp ₁	S
	<i>C.tag</i>	Sp ₁	Sp ₁	Sp ₁	U	Sp ₁	U	S
	<i>S.alb</i>	U	U	U	U	S	U	S
<i>S.alb</i>	<i>B.gym</i>	Sp ₁	Sp ₁	Sp ₁	Sp ₁	Sp ₁	Sp ₁	S
	<i>A.mar</i>	Sp ₁	Sp ₁	Sp ₁	Sp ₁	Sp ₁	Sp ₁	S
	<i>C.tag</i>	Sp ₁	Sp ₁	Sp ₁	Sp ₁	Sp ₁	Sp ₁	S
	<i>R.muc</i>	U	U	U	U	S	U	S

The inequalities that are used to evaluate the outcomes of the phase plane graphs are shown in Table 6. Simulation results of the same combination of species interactions subjected to different perturbations may exhibit alternative an equilibrium state, for instance, from unstable to stable. Refer to Table 1 for abbreviations. K_1 and K_2 refer to carrying capacity of species 1 and 2, respectively; a_{12} and a_{21} are the competition coefficients made up of more mechanistic parameters (see eqn (7)). Acronyms represent an unstable equilibrium (U), species 1 wins (Sp₁), species 2 wins (Sp₂) and stable equilibrium (S).

Table 6: Summary of inequalities that are used to interpret Table 5 according to the four classical outcomes of the phase plane antalysis.

Inequalities	$K_1 > K_2/a_{21}$	$K_1 < K_2/a_{21}$
$K_2 > K_1/a_{12}$	Unstable equilibrium (U)	Species 2 wins (Sp ₂)
$K_2 < K_1/a_{12}$	Species 1 wins (Sp ₁)	Stable equilibrium (S)

Refer to Table 5 for K_1 , K_2 , a_{12} and a_{21} .

To evaluate the variation in the model predictions due to stochasticity, we repeated the procedure of determining model predictions 15 times using the same model parameters for each run. The variances of the population density trajectories for the replicated simulations did not vary significantly ($p > 0.05$) and so the output curves were considered to adequately illustrate the model runs.

3.4 Sensitivity analysis of disturbance magnitudes

The summary results for 25%, 50%, 75% and 90% disturbance impacts based mainly on the peak population densities are presented for *A. marina*, *B. gymnorrhiza*, *C. tagal*, *R. mucronata* and *S. alba* species interactions, respectively, in the different mangrove stands of *A. marina*, *B. gymnorrhiza*, *C. tagal*, *R. mucronata*, *S. alba*, *R. mucronata/A. marina* and *R. mucronata/C. tagal*.

For a 25% scale of disturbance, *A. marina* registered the highest population density trajectory peaking at 60% when interacting with *B. gymnorrhiza*. For a 50% disturbance, *A. marina* emerged dominant and re-colonised fastest when in a *C. tagal* stand, which finally registered the highest population density trajectory on recovery. The recovery is slowest when *A. marina* is in an *R. mucronata/A. marina* or *R. mucronata/C. tagal* stand. When subjected to a 75% and further a 90% disturbance, *A. marina* appeared most dominant when interacting with *B. gymnorrhiza*. However, by the end of the simulations for the latter two categories of disturbance, the recovery had not yet stabilised.

After a 25% disturbance, *B. gymnorrhiza* is most dominant when paired with *R. mucronata* when in a *R. mucronata* and *A. marina* stand. *B. gymnorrhiza* dominates by 20–80% in its interaction with *R. mucronata*. Comparatively, *B. gymnorrhiza* is least competitive when paired with *R. mucronata/A. marina* where its population density is 10% only. When the simulation is subjected to a 50% disturbance, *B. gymnorrhiza* is found to be most dominant when interacting with *R. mucronata* and its population peaks at over 90%. As at the previous disturbance level, *B. gymnorrhiza* is least competitive when paired with *R. mucronata/A. marina*. When subjected to both 75% and 90% disturbances, there is no full recovery for any of the pairwise interactions by the end of the simulations and this is evident as the trajectories continue to rise.

C. tagal registers the fastest rate of population increase when paired with *A. marina* after being subjected to a 25% disturbance achieving a peak of about 80%. Its lowest population density values are during its interactions with *R. mucronata/A. marina* and *R. mucronata/C. tagal*. When subjected to a 50% disturbance, similar trends are seen although the peak value is 50% which is recorded for *C. tagal* and *A. marina* interaction. There is no outright dominance of either species in this simulation. In the case of a 75% disturbance, *C. tagal* records the highest trajectory of population density with *A. marina*. The peak value of *C. tagal* is, however, low, approximately 40%. For the 90% disturbance, *C. tagal* and *A. marina* pairing yields the highest population density values for *C. tagal*, which is only about 10%.

R. mucronata registers the highest value of population density when paired with *A. marina* with a peak of almost 100% following a 25% disturbance. For the 50% disturbance simulation, similar results were registered, though the peak population density of *R. mucronata* is approximately 70%. The simulation of the 75% disturbance scenario is also similar with the peak density of *R. mucronata* being further reduced to 50%. In the 90% disturbance, the simulation shows an emerging dominance of *R. mucronata* in its interactions with *C. tagal* and *S. alba*.

For *S. alba* interactions, *S. alba* and *B. gymnorrhiza*, *S. alba* and *R. mucronata/A. marina* and *S. alba* and *R. mucronata/C. tagal* register the highest trajectories for *S. alba* of about 80% each for the simulation of a 25% disturbance. The cases for the other categories of disturbance that 50%, 75% and 90% indicate no stabilisation in recovery of *S. alba* for all categories at the end of the simulation.

The results are dominated by clustered trajectories without clear dominant interaction pairs of mangrove species. Generally, for each magnitude of disturbance, *S. alba* records the highest trajectory of population density with a different pairwise mangrove species.

In general, the simulation outputs indicated changes in the gradients of the population density trajectories and longer periods to attain steady state for higher disturbance levels.

3.5 Simulation experiments on the effects of canopy disturbances on forest succession

The gradients of simulations for 20% disturbance were generally different from the 60% disturbed areas in terms of the population density magnitudes although their trajectory curves were ultimately similar in most cases. Figure 4 shows the simulation outputs for *B. gymnorrhiza* in response to disturbance events of 20% and 60% scales. Other simulation outputs that were realised included *A. marina*, *C. tagal*, *R. mucronata* and *S. alba*. although the graphical versions are not presented in this paper. The population density trajectories due to the disturbance effects on various pairwise

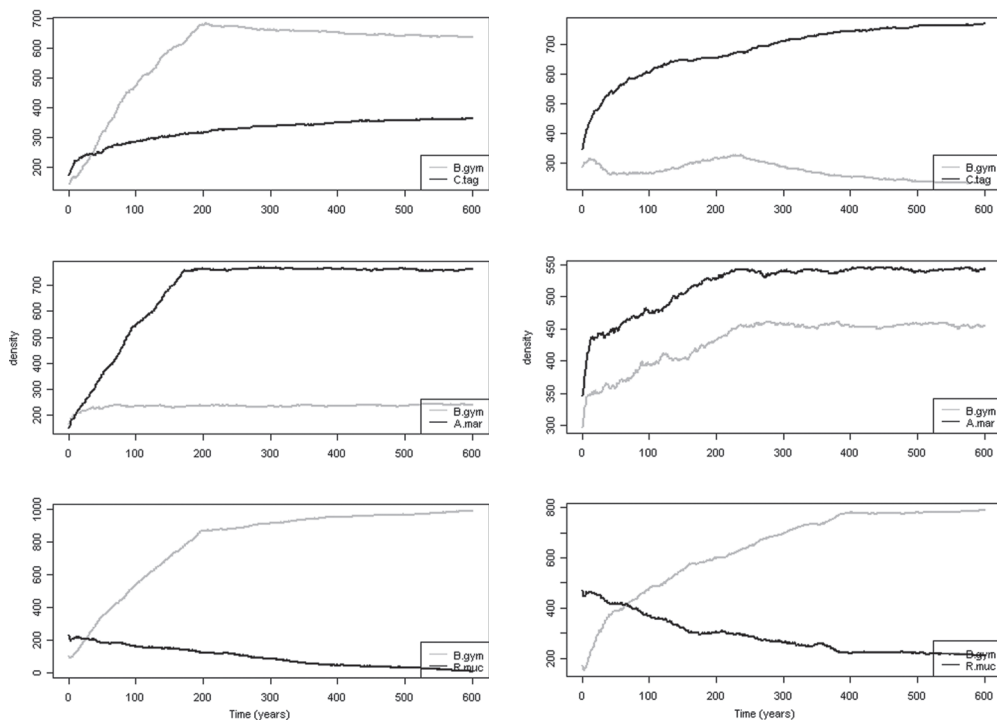


Figure 4: Evolution of population density of *Bruguiera gymnorrhiza*, in pairwise interactions with other mangrove species, in function of spatial and temporal changes in Gazi Bay that were simulated for 20% disturbance scenarios (left-hand side graphs) and 60% disturbance scenarios (right-hand side graphs). The X-axis represents the time steps and the Y-axis the population density. In the graphs, *B.gym* = *Bruguiera gymnorrhiza*, *C.tag* = *Ceriops tagal*, *A.mar* = *Avicennia marina*, *R.muc* = *Rhizophora mucronata*, *S.alba* = *Sonneratia alba*, *R.muc/A.mar* = *Rhizophora mucronata/Avicennia marina*, *R.muc/C.tag* = *Rhizophora mucronata/Ceriops tagal*.

combinations were also summarily ranked for each stand interactions and the trends shown were occasionally different (for the same pairwise combinations) when the disturbance magnitude was altered from 20% to 60%.

The simulation results in the *B. gymnorrhiza* stand indicate that for *B. gymnorrhiza* and *C. tagal* interaction (20% disturbance impact), *C. tagal* emerges dominant eventually with a 70% population density of occupied cells. For the 60% disturbance impact (Fig. 4), *B. gymnorrhiza* eventually outcompetes *C. tagal*. For *B. gymnorrhiza* and *A. marina* simulation, the case of 20% disturbance (Fig. 4) shows *A. marina* eventually dominates by 45–55% of *B. gymnorrhiza*. For the 60% disturbance, *A. marina* emerges superior by 75% compared to 25% of *B. gymnorrhiza*. *B. gymnorrhiza*, although with a lower initial density, ends up as the superior competitor for both disturbance scenarios in its interaction with *R. mucronata*. *S. alba* outcompetes *B. gymnorrhiza* for in both disturbance scenarios. Overall, *B. gymnorrhiza* emerges as the inferior competitor in its interactions with *R. mucronata/A. marina* and similarly with *R. mucronata/C. tagal*. The results of the simulation outputs for all the stands are summarised in Table 7.

In the rankings, the summarised outputs of *B. gymnorrhiza* for the 20% disturbance impacts indicate that, comparatively for all the interacting species, *B. gymnorrhiza* records the highest population density trajectory when interacting pairwise with *R. mucronata*. The lowest trajectory of *B. gymnorrhiza* simulations occurs when it is paired with *S. alba*, with *B. gymnorrhiza* ending up with a population density of 20% and *S. alba* 80%. Similarly, for summarised *B. gymnorrhiza*-related outputs for the 60% disturbance scenario, *B. gymnorrhiza* records the highest population density trajectory in its pairwise relationships with *C. tagal* and *R. mucronata*, while *B. gymnorrhiza*'s lowest population trajectory occurs when it is paired with *R. mucronata/C. tagal*.

Table 7: Summary table illustrating predicted scenarios at the end of the model simulations subject to 20% and 60% disturbance events.

Species	Mangrove species/assemblages														
	<i>B.gym</i>		<i>A.mar</i>		<i>C.tag</i>		<i>R.muc</i>		<i>S.alb</i>		<i>R.muc/A.mar</i>		<i>R.muc/C.tag</i>		
	20%	60%	20%	60%	20%	60%	20%	60%	20%	60%	20%	60%	20%	60%	
<i>B.gym</i>	–	–	^a L	L	L	^b W	W	W	L	L	L	L	L	L	W
<i>A.mar</i>	W	W	–	–	L	L	L	L	L	L	L	L	L	L	L
<i>C.tag</i>	L	L	W	W	–	–	W	L	L	L	L	L	L	L	L
<i>R.muc</i>	L	L	W	W	L	W	–	–	L	L	L	L	L	L	L
<i>S.alb</i>	W	W	W	L	W	W	W	W	–	–	L	W	W	W	W

The columns represent the mangrove species/assemblage stands. The rows indicate the main species that are considered in the simulations in each of the mangrove/assemblages stands shown in the columns and the data matrix indicates the predictions. The results that have borders reflect situations where changes in disturbance impact magnitudes produce a different dominant species. Refer to Table 1 for abbreviations. ^aL = lost (or floristic extinction *sensu* Dahdouh-Guebas and Koedam [80]); ^bW = won (or floristic dominance *sensu* Dahdouh-Guebas and Koedam [80]). Lost implies that the mangrove species indicated in a row are predicted to be outcompeted at the end of the simulation by the species/assemblage it is paired with which is indicated in the column. Won indicates that the mangrove species listed in the row are predicted to dominate the competition against the species/assemblage that it is paired against in the column at the end of the simulation. Inconclusive implies that there is no outright dominance by either competitor.

4 DISCUSSION

4.1 Forest structure description

The importance value gives an indication of (1) how frequently a species is encountered throughout the forest (relative frequency), (2) its abundance (relative density) and (3) how large its individuals are (relative dominance) in relation to all the other species encountered in the sample. The sum of these values is an indication of the overall importance of a given species. According to Binkley *et al.* [81], changes in stand structure allow dominant trees to sustain high rates of growth by increasing their acquisition of resources, whereas smaller, non-dominant trees grow more slowly as a result of their more limited acquisition of resources and use the resources acquired less efficiently than the dominant ones.

Determining the vegetation characteristics of Gazi Bay was a crucial step in obtaining the parameterisation data for the CA model. The PCQM approach was suitable for this study due to the amount of ground covered which enabled sampling of many transects in at least each of the vegetation assemblages [60]. However, for future transect surveys, it would be prudent to use plot-based approaches for data collection of the mangrove species structural attributes. This is due to advantages, such as replication of ground truth data collection such that the same plots are re-sampled and the potential to implement model from a spatial explicit perspective for production of predictive Geographic Information Systems map outputs.

4.2 Sensitivity and analysis of the Lotka–Volterra competition model

In this study, a sensitivity analysis test was also carried out to analyse the impacts due to various magnitudes of disturbance events at 25%, 50%, 75% and 90% levels. The simulation outputs showed that the highest and lowest population density trajectories did not always feature the same interacting pairs and that the species dominance alternated at different levels of disturbances. For instance, Overpeck *et al.* [82], in their model simulations of species composition in North American forests which were subjected to climate change, found that when the degree of disturbance was increased after a certain period, the simulation results showed varied biomass changes of the forest species different from the pre-disturbance period. The findings reflect empirical expectations and suggest that disturbance may influence successional trends though this can only be corroborated by further investigations. Pickett and White [83] argued that disturbances play a central role in determining the distribution and abundance of tree species in forests. Disturbances create canopy openings that provide the opportunity for tree recruitment [21]. Several studies have suggested that canopy gaps may be important in the establishment, recruitment and growth of mangroves [21, 84–90]. It is important to note that varying the degree of disturbance impacts may affect the equilibrium status of the mangrove ecosystem since the competition coefficients may be altered thus affecting the coexistence ratios. The phase plane analysis results suggest that for the simulations, interacting species composition may be considered important in determining the temporal stability in Gazi. There is a need to evaluate some inherent factors through transient dynamics analysis which could enhance the predictions.

Although the sensitivity analysis gives useful information that may provide guidelines for future research, it could probably be worthwhile to couple this study with investigating the effects from possible contributory factors to the observed evolutionary patterns since studies have shown that competition for one resource usually affects the ability of an organism to exploit another resource [75]. For example, there may be interdependence between competition for space and food and different disturbance regimes may cause variations in availability and ability of resource exploitation

by species. When a colony of one species interacts with a colony of another species, it may cause food shortage to the other which could reduce the ability of the second species to compete for space. Among rooted plants, if one species invades the canopy of another and deprives it of light, the suppressed species will suffer directly from the reduction in light energy that it receives, but this will also reduce the rate of root growth causing it to be less able to exploit the supply of water and nutrients in the soil. This further reduces its rate of shoot and leaf growth [75].

Some documented findings regarding disturbances and their impacts in Gazi indicate that clear-felled areas did not show any natural regeneration [57, 91, 92]. Dahdouh-Guebas *et al.* [17] and Kairo *et al.* [93] found that the regeneration does not necessarily result in the same species being harvested. In Mida creek, they observed that in a mixed stand of *C. tagal* and *R. mucronata*, there was a tendency for natural regeneration to favour *C. tagal*, irrespective of the harvested species. Obade *et al.* [94], using change detection methods, also observed a similar trend in the north-western area of Gazi that *R. mucronata* was replaced by *C. tagal* in 1992 in comparison to the coverage of 1965, which may be attributable to the more harsh soil conditions after erosion. Clear felling of mangroves is thought to greatly impair natural regeneration due to resulting unfavourable site conditions according to Bosire *et al.* [57], which can, however, be mitigated [54]. These are a few empirical observations that relate to our modelling outputs illustrating that disturbance events can trigger recolonisation by a different species in the impacted area. However, it was not feasible to ascertain whether or not these changes were permanent as this requires empirical corroboration. Heavy rains contribute directly to loss of mangrove area, e.g. the El Niño rains of 1997/1998 which resulted in heavy sedimentation, killed mature *Rhizophora* trees in Gazi Bay though a reforestation programme was initiated in the affected area.

4.3 Disturbance modelling

When a landscape experiences a disturbance, the impact is usually not uniform throughout. In fact, disturbances generally create complex heterogeneous patterns across landscapes in which some areas may be affected and not others, and the severity of the disturbance is likely to vary within the affected area. At the patch scale, e.g. a clear-cut area, a disturbance may destroy biomass, homogenise plant species composition and disorganise established patterns of growth and competition [95]. The extent of the impact due to clear cutting may result in only a few species re-establishing in a stand characterised by little competitive interaction.

Changes in population size have often been attributed to mechanisms such as disturbances, variability of environmental factors and pathogens [96, 97]. The results of *B. gymnorrhiza* simulations indicated different pairwise relationships registered for the highest trajectories of population densities for the two levels of disturbances, i.e. 20% (paired with *R. mucronata*) and 60% (paired with *C. tagal* and *R. mucronata*) categories. For the lowest *B. gymnorrhiza* population densities, different pairwise relationships were observed for the different disturbance levels. Similarly, *S. alba* has different results of pairwise relationships that register the highest population density trajectories for the two magnitudes of disturbance. The results of *A. marina*, *R. mucronata* and *C. tagal* simulations were similar for the different disturbance events of 20% and 60%, even though the population density proportions varied. This is consistent with the hypothesis that the varying scales of disturbance may lead to different outputs for the same pairwise simulation which suggests implications on successional trends in such an area. A particular disturbance observed at one scale may be a disruptive force, yet at a different scale, it may be a stabilising force. Thom [98, 99], in his reviews of mangrove succession, emphasised the stability of specific intertidal zones and the lack of any temporal sequence in the regeneration of mangrove zones following a disturbance. Begon *et al.* [75] argue that gaps of

unoccupied space occur unpredictably after being created by a disturbance. When these gaps are recolonised, the first species to do so is not necessarily the one that is best able to exclude other species in the long term. The species that is initially slower to invade the gaps created outcompetes and eventually excludes the other species (despite the superiority of this species) from that gap.

Some important ecological effects of disturbance and the subsequent patterns of succession are the legacies and residuals that remain after the disturbance [33]. Residuals are organisms or propagules which survive a disturbance event. These may be used to infer severity or be taken as an index of intensity. The ecological legacies may be categorised as biotic (residuals) or abiotic. Biotic legacies or residuals refer to the types, quantities and patterns of organisms and biotic structures that persist from the pre-disturbance ecosystem. Residuals, therefore, may comprise surviving individuals, standing dead trees and vegetative tissues that can regenerate. Abiotic legacies refer to the physical modification of the environment that may result from the disturbance, such as erosion or mudslides. Understanding the nature of disturbance mosaic and the factors controlling these landscape patterns is therefore additionally useful for predicting ecosystem dynamics and vegetation development in disturbance-prone landscapes. To get such information *a priori* remains elusive as the field-based studies need to cover a few generations and thus potentially too expensive logistically.

The two mangrove simulation models FORMAN [44] and KiWi [46, 47] have already been used to demonstrate both the existence of different successional stages and succession trajectories in mangrove forests depending on the type of disturbances, the frequency and the overall environmental conditions. Both models describe space in all three dimensions and individual trees in their local neighbourhood constellation [45]. Such sophisticated models provide several advantages: they can consider a heterogeneous nutrient availability, seed dispersal in real landscapes, etc. Their parameterisation, however, requires many site-specific quantitative data that are scanty in Gazi Bay. Since most models face myriad problems related to parameterisation (but see [45]), it was important for this case study to find a compromise between using simplistic parameterisations and expanding gap models with physiology-based functions and parameters that are difficult to estimate [100]. This study fulfilled this aim by using the available information and data most effectively. Although the model presented is rather simple in its structure, it provided valuable insights into the complexity of potential succession trajectories in Gazi Bay depending on species dominance, seed dispersal and intensity of disturbances.

5 CONCLUSIONS

CA models based on the Lotka–Volterra model of competition are good proxies for providing connections between patterns and processes of competing mangrove species and also predicting spatial–temporal variations in the aftermath of disturbance events. A useful approach to study forest dynamics is to develop a generalised model, such as our approach, that can be easily parameterised to simulate dynamics in many different forests and this is consistent with the proposals of Shugart [101] and Urban *et al.* [102]. The approach applied in this study is unique and advantageous from many model-based methods because it considers the important parameter inputs and is cost effective, where all forcing functions, for instance abiotic and biotic factors, are inferred through the simulations based on the forest structural attributes data. It is noteworthy that mangrove ecosystems can no longer provide their full ecological services as a consequence of degradation, thus incur a socio-economic cost that can be felt both locally and globally; for instance, there are reduced fish catches, food security and tourism revenue in coastal communities, loss of export earnings and decline in the tourism industry and increased coastal erosion and destruction from storms and catastrophic natural events [13].

Normally, site productivity and resource availability control the rate of return to pre-disturbance conditions on a patch. However, the uncertainties regarding residuals or biotic legacies after a disturbance event provide a constraint for the model since these may only be accounted for, in the simulations, using empirical observations over a long period. Due to the important ecological consequences due to disturbance, it is prudent that future experimental designs to study Gazi mangroves be specifically focussed on tree recruitment and its scale, intensity and spatial patterns of tree mortalities in response to specific types of disturbance events or regimes. Future transient dynamics assessment of Gazi mangroves should be carried out on a regular basis to obtain reliable input parameters for the model. This would enhance the present knowledge of forest dynamics which may be considered to have uncertainties without a comprehensive understanding of the disturbance regime.

From a modelling point of view, the novelty of the approach used in this study lays in its cost effectiveness and in its consideration for important parameter inputs based on a large set of real data (>1100 records) from forest structural attributes such as the importance value of the tree species. More important is that this approach has never been used in a mangrove and that its results have the ability to forecast 600 years of ecological dynamics in the mangrove. Although this time frame is too long to adopt in contemporary management of mangroves, it certainly offers scientific data and insight for further theoretical biological modelling of ecodynamics and disturbances.

ACKNOWLEDGEMENTS

This study was made possible through a fellowship from the Vrije Universiteit Brussel Advice Council for Development granted to Paul Obade and through research grants financed by VUB and ULB universities, the science foundations FWO-Vlaanderen and the Fonds de la Recherche Scientifique – FNRS, and the EC funded project PUMPSEA (FP6 – INCO contract no. 510863). We are grateful to Dr Johnson Kazungu (Director, KMFRI) and the people of Gazi for facilitating logistical support.

REFERENCES

- [1] Twilley, R.R., Chen, R. & Hargis, T., Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystem. *Water, Air and Soil Pollution*, **64**, pp. 265–288, 1992.
- [2] Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. & Srivastava, D.S., Extinction and ecosystem function in the marine benthos. *Science*, **306**, pp. 1177–1180, 2004.
- [3] Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J., Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, pp. 207–251, 2004.
- [4] Kristensen, E., Bouillon, S., Dittmar, T. & Marchand, C., Organic carbon dynamics in mangrove ecosystems: a review. *Aquatic Botany*, **89(2)**, pp. 201–219, 2008.
- [5] Aburto-Oropeza, O., Ezcurra, E., Danemann, G., Valdez, V., Murria, J. & Sala, E., Mangroves in the Gulf of California increase fishery yields. *Proceedings of the National Academy of Sciences of the United States of America*, **105(30)**, pp. 10456–10459, 2008.
- [6] Cannicci, S., Burrows, D., Fratini, S., Lee, S.Y., Smith III, T.J., Offenberg J. & Dahdouh-Guebas, F., Faunistic impact on vegetation structure and ecosystem function in mangrove forests: a review. *Aquatic Botany*, **89(2)**, pp. 186–200, 2008.
- [7] Nagelkerken, I., Blaber, S., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.O., Pawlik, J., Penrose, H.M., Sasekumar, A. & Somerfield, P.J., The habitat function of mangroves for terrestrial and marina fauna: a review. *Aquatic Botany*, **89(2)**, pp. 155–185, 2008.

- [8] Walters, B.B., Rönnbäck, P., Kovacs, J., Crona, B., Hussain, S., Badola, R., Primavera, J.H., Barbier, E.B. & Dahdouh-Guebas, F., Ethnobiology, socio-economics and adaptive management of mangroves: a review. *Aquatic Botany*, **89(2)**, pp. 220–236, 2008.
- [9] Badola, R., Hussain, S.A., Valuing ecosystem functions: an empirical study on the storm protection function of Bhitarkanika mangrove ecosystem, India. *Environmental Conservation*, **32(1)**, pp. 85–92, 2005.
- [10] Dahdouh-Guebas, F., Jayatissa, L.P., Di Nitto, D., Bosire, J.O., Lo Seen D. & Koedam, N., How effective were mangroves as a defence against the recent tsunami? *Current Biology*, **15(12)**, pp. R443–447, 2005.
- [11] Gilman, E., Ellison, J., Duke, N.C. & Field, C., Threats to mangroves from climate change and adaptation options: a review. *Aquatic Botany*, **89(2)**, pp. 237–250, 2008.
- [12] Burke, L. & Maidens, J. (eds), *Reefs at Risk in the Caribbean*, World Resources Institute: Washington, 2004.
- [13] UNEP-WCMC, *In the Front Line: Shoreline Protection and Other Ecosystem Services from Mangroves and Coral Reefs*, United Nations Environment Programme, World Conservation Monitoring Centre: Cambridge, 2006.
- [14] Farnsworth, E.J. & Ellison, A.M., The global conservation status of mangroves. *Ambio*, **26**, pp. 328–334, 1997.
- [15] Semesi, A.K. Mangrove management and utilization in Eastern Africa. *Ambio*, **27**, pp. 620–626, 1998.
- [16] Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, C.M., Clay, J., Folke, C., Lubchenco, J., Moony, H. & Troell, M., Effect of aquaculture on world fish supplies. *Nature*, **405**, pp. 1017–1024, 2000.
- [17] Dahdouh-Guebas, F., Verheyden, A., De Genst, W., Hettiarachchi, S. & Koedam, N., Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography: a case study in Galle. *Bulletin of Marine Science*, **67**, pp. 741–759, 2000.
- [18] Kairo, J.G. (ed.), *Ecology and Restoration of Mangrove Systems in Kenya*. PhD dissertation, Vrije Universiteit Brussel: Brussels, 2001.
- [19] Duke, N.C., Meynecke, J.O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I. & Dahdouh-Guebas, F., A world without mangroves? *Science*, **317**, pp. 41–42, 2007.
- [20] Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyachchi, S., Jayatissa, L.P. & Koedam, N., Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. *Current Biology*, **15**, pp. 579–586, 2005.
- [21] Sherman, R.E., Fahey, T.J. & Battles, J.J., Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. *Journal of Ecology*, **88**, pp. 165–178, 2000.
- [22] Saenger, P. (ed.), *Mangrove Ecology, Silviculture and Conservation*, Kluwer Academic Publishers: Dordrecht, 2002.
- [23] Zavaleta, E.S. & Hulvey, K.B., Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science*, **306**, pp. 1175–1177, 2004.
- [24] Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. & Watson, R., Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**, pp. 787–790, 2006.
- [25] White, P.S. & Pickett, S.T., Natural disturbance and patch dynamics: an introduction. *The Ecology of Natural Disturbance and Patch Dynamics*, eds. S.T.A. Pickett & P.S. White, Academic Press: New York, pp. 3–13, 1985.

- [26] Watt, A.S., Pattern and process in the plant community. *Journal of Ecology*, **35**, pp. 1–22, 1947.
- [27] White, P.S., Pattern, process, and natural disturbance in vegetation. *Botanical Review*, **45**, pp. 229–299, 1979.
- [28] Perry, G.L.W., Landscapes, space and equilibrium: shifting viewpoints. *Progress in Physical Geography*, **26**, pp. 339–359, 2002.
- [29] Laurie, W.A. & Brown, D., Population Biology of Marine Iguanas (*Amblyrhynchus-Cristatus*). Factors Affecting Survival. *Journal of Animal Ecology*, **59**, pp. 545–568, 1990.
- [30] Romme, W.H., Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs*, **52**, pp. 191–221, 1982.
- [31] Turner, G.M., Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics*, **20**, pp. 171–197, 1989.
- [32] Baker, W.L., Effect of scale and spatial heterogeneity on fire-interval distributions. *Canadian Journal of Forest Research*, **19**, pp. 700–706, 1989.
- [33] Turner, G.M. & Dale, V.H., Comparing large, infrequent disturbances; what have we learned? Introduction for special feature. *Ecosystems*, **1**, pp. 493–496, 1998.
- [34] Collins, S. L., Knapp, A. K., Briggs, J.M. & Steinhauer, E.M., Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, **280**, pp. 745–747, 1998.
- [35] Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B., Catastrophic shifts in ecosystems. *Nature*, **413**, pp. 591–596, 2001.
- [36] Turner, G.M., Gardner, R.H. & O’Neill, R.V., *Landscape Ecology: In theory and practise: pattern and process*. Springer-Verlag, New York, 2001.
- [37] Higgins, S.I., Turpie, J.K., Costanza, R., Cowling, R.M., Le Maitre, D.C., Marais, C. & Midgley, G.F., An ecological economic simulation model of mountain fynbos ecosystems: Dynamics, valuation and management. *Ecological Economics*, **22**, pp. 155–169, 1997.
- [38] Harper, J.L. (ed.), *Population Biology of Plants*, Academic Press: London, 1977.
- [39] Mack, R.N. (ed.), *Invading Plants: Their Potential Contribution to Population Biology*, Academic Press: London, 1985.
- [40] Richardson, D.M. & Bond, W.J., Determinants of plant distribution: Evidence from pine invasions. *American Naturalist*, **137**, pp. 639–668, 1991.
- [41] Lodge, D.M. Biological invasions: Lessons for ecology. *Trends in Ecology and Evolution*, **8**, pp. 133–137, 1993.
- [42] Busing, R.T. & Maily, D., Advances in spatial, individual-based modelling of forest dynamics. *Journal of Vegetation Science*, **15**, pp. 831–842, 2004.
- [43] Sprugel, D.G. Disturbance, Equilibrium, and environmental variability – what is natural vegetation in a changing environment. *Biological Conservation*, **58**, pp. 1–18, 1991.
- [44] Chen, R. & Twilley, R.R., A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. *Journal of Ecology*, **86**, pp. 37–51, 1998.
- [45] Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N., Fontalvo, M., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C. & Twilley, R.R., Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: a review. *Aquatic Botany*, **89(2)**, pp. 260–274, 2008.
- [46] Berger, U., Adams, M., Grimm, V. & Hildenbrandt, H., Modelling secondary succession of neotropical mangroves: Causes and consequences of growth reduction in pioneer species. *Perspectives in Plant Ecology, Evolution and Systematics* **7**, pp. 243–252, 2006.
- [47] Berger, U. & Hildenbrandt, H., A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. *Ecological Modelling*, **132**, pp. 287–302, 2000.

- [48] Durrett, R. & Levin, S., The importance of being discrete (and spatial). *Theoretical Population Biology*, **46**, pp. 363–394, 1994.
- [49] Kawata, M. & Toquenaga, Y., From artificial individuals to global patterns. *Trends in Ecology and Evolution*, **9**, pp. 417–421, 1994.
- [50] Parrott, L. Quantifying the complexity of simulated spatiotemporal population dynamics. *Ecological Complexity*, **2(2)**, pp. 175–184, 2005.
- [51] Comins, H.N. & Hassell, M.P., The dynamics of predation and competition in patchy environments. *Theoretical Population Biology*, **31**, pp. 393–421, 1987.
- [52] Tilman, D., The importance of the mechanisms of interspecific competition. *American Naturalist*, **129**, pp. 769–774, 1987.
- [53] Kairo, J.G., Dahdouh-Guebas, F., Bosire, J. & Koedam, N., Restoration and management of mangrove systems – A lesson for and from the East African region. *South African Journal of Botany*, **67**, pp. 383–389, 2001.
- [54] Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G. & Koedam, N., Functionality of restored mangroves: a review. *Aquatic Botany*, **89(2)**, pp. 251–259, 2008.
- [55] Verheyden, A. (ed.), Rhizophora mucronata wood as a proxy for changes in environmental conditions. A study of the wood anatomy, stable isotope chemistry and inorganic composition of a Kenyan mangrove species. PhD thesis, Vrije Universiteit Brussel: Brussels, 2004.
- [56] Dahdouh-Guebas, F., Verneirt, M., Cannicci, S., Kairo, J.G., Tack, J.F. & Koedam, N., An exploratory study on grapsid crab zonation in Kenyan mangroves. *Wetlands Ecology and Management*, **10**, pp. 179–187, 2002.
- [57] Bosire, J., Dahdouh-Guebas, F., Kairo, J.G. & Koedam, N., Colonisation of non-planted mangrove species into restored mangrove stands in Gazi Bay, Kenya. *Aquatic Botany*, **76**, pp. 267–279, 2003.
- [58] Cottam, G. & Curtis J.T., The use of distance measures in phytosociological sampling. *Ecology*, **37**, pp. 451–460, 1956.
- [59] Cintrón, G. & Schaeffer-Novelli, Y., Methods for studying mangrove structure. *The Mangrove Ecosystem: Research Methods*, eds S.C. Snedaker & J.G. Snedaker, UNESCO: Paris, pp. 91–113, 1984.
- [60] Dahdouh-Guebas, F. & Koedam, N., Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): solutions to ambiguous field situations and description of the PCQM + protocol. *Forest Ecology and Management*, **228**, pp. 1–18, 2006.
- [61] Neukermans, G., Dahdouh-Guebas, F., Kairo J.G. & Koedam, N., Mangrove species and stand mapping in Gazi Bay (Kenya) using Quickbird satellite imagery. *Journal of Spatial Science*, **52(1)**, pp. 75–86, 2008.
- [62] Brokaw, N. & Thompson, J., The H for DBH. *Forest Ecology and Management*, **129**, pp. 89–91, 2000.
- [63] Holdridge, L., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. (eds), *Forest Environment in Tropical Life Zones*, Pergamon Press: New York, 1971.
- [64] Blanco, J.F., Bejarano, J.L. & Cantera, J.R., A new look at computation of the complexity index in mangroves: do disturbed forests have clues to analyse canopy height patchiness? *Wetlands Ecology and Management*, **9**, pp. 91–100, 2001.
- [65] Curtis, J.T. (ed.), *The Vegetation of Winsconsin. An Ordination of Plant Communities*, University of Winsconsin Press: Madison, 1959.
- [66] Wilson, W. (ed.), *Simulating Ecological and Evolutionary Systems*, Cambridge University Press: Cambridge, 2000.

- [67] Calow, P., Falk, D.A., Grace, J., Moore, P.D., Shorrocks, B. & Stearn, S.C. (eds), *The Encyclopedia of Ecology and Environmental Management*, Blackwell Science: Oxford, 1998.
- [68] Hastings, A., Disturbance, coexistence, history and competition for space. *Theoretical Population Biology*, **18**, pp. 363–373, 1980.
- [69] Hastings, A., Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology*, **74**, pp. 1362–1372, 1993.
- [70] Turner, G.M., Romme, W.H., Gardner, R.H., O'Neill, R.V. & Kratz, T.K., A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecology*, **8**, pp. 213–227, 1993.
- [71] Lehman, C.L. & Tilman, D., Biodiversity, stability and productivity in competitive communities. *The American Naturalist*, **156**(5), pp. 534–552, 2000.
- [72] Rozdilsky, I.D. & Stone, L., Complexity can enhance stability in competitive systems. *Ecology Letters*, **4**, pp. 397–400, 2001.
- [73] Pascual, M., Roy, M. & Franc, A., Simple temporal models for ecological systems with complex spatial patterns. *Ecology Letters*, **5**, pp. 412–419, 2002.
- [74] Hastings, A., Transients: the key to long-term ecological understanding? *Trends in Ecology and Evolution* **19**, pp. 39–45, 2004.
- [75] Begon, M., Harper, J.L. & Townsend, C.R. (eds), *Ecology: Individuals, Populations, and Communities*, 3rd edn, Blackwell Science Ltd.: Cambridge, 1996.
- [76] Jeltsch, F., Milton, S.J., Dean, W.R.J. & van Rooyen, N., Tree spacing and coexistence in semiarid savannas. *Journal of Ecology*, **84**, pp. 583–595, 1996.
- [77] Swartzman, G.L. & Kaluzny, S.P. (eds), *Ecological Simulation Primer*, Macmillan: New York, 1987.
- [78] McCallum, H. (ed.), *Population Parameters: Estimation for Ecological Models*, Blackwell Science: Oxford, 2000.
- [79] Soetaert, K., deClippele, V. & Herman, P., Femme, a flexible environment for mathematically modelling the environment. *Ecological Modeling*, **151**, pp. 177–193, 2002.
- [80] Dahdouh-Guebas, F. & Koedam, N., A synthesis of existent and potential mangrove vegetation structure dynamics from Kenyan, Sri Lankan and Mauritanian case-studies. *Mededelingen der Zittingen van de Koninklijke Academie voor Overzeese Wetenschappen / Bulletin des Séances de l'Académie Royal des Sciences d'Outre-Mer*, **48**, pp. 487–511, 2002.
- [81] Binkley, D., Stape, J.L., Ryan, M.G., Barnard, H.R. & Fownes, J., Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. *Ecosystems*, **5**, pp. 58–67, 2002.
- [82] Overpeck, J.T., Rind, D. & Goldberg, R., Climate-Induced Changes in Forest Disturbance and Vegetation. *Nature*, **343**, pp. 51–53, 1990.
- [83] Pickett, S.T.A. & White, P.S. (eds), *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press Inc.: New York, 1985.
- [84] Rabinowitz, D., Mortality and initial propagule size in mangrove seedlings in Panama. *Journal of Ecology*, **66**, pp. 45–51, 1978.
- [85] Ball, M.C., Patterns of secondary succession in a mangrove forest of South Florida. *Oecologia*, **44**, pp. 226–235, 1980.
- [86] Jimenez, J.A., The structure and function of dry weather mangroves on the Pacific coast of Central America with an emphasis on *Avicennia bicolor* forests. *Estuaries* **13**, pp. 182–192, 1990.
- [87] Roth, L.C., Hurricanes and Mangrove Regeneration - Effects of Hurricane Joan, October 1988, on the Vegetation of Isla Del Venado, Bluefields, Nicaragua. *Biotropica*, **24**, pp. 375–384, 1992.

- [88] Baldwin, A.H., Platt, W.J., Gathen, K.T., Lessman, J.M. & Rauch, T.J., Hurricane damage and regeneration in fringe forests of southeast Florida, USA. *Journal of Coastal Research*, **S12**, pp. 169–183, 1995.
- [89] Duke, N.C., Ball, M.C. & Ellison, J.C., Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, **7**, pp. 27–47, 1998.
- [90] Baldwin, A., Egnotovitch, M., Ford, M., Platt, W., Regeneration in fringe mangrove forests damaged by Hurricane Andrew. *Plant Ecology*, **157**, pp. 149–162, 2001.
- [91] Kairo, J.G. (ed.), *Community Participatory Forestry for Rehabilitation of Deforested Mangrove Areas of Gazi Bay (Kenya). A First Approach*, Final technical report, University of Nairobi, Nairobi, 1995.
- [92] Dahdouh-Guebas, F., Van Pottelbergh, I., Kairo, J.G., Cannicci, S. & Koedam, N., Human-impacted mangroves in Gazi (Kenya): predicting future vegetation based on retrospective remote sensing, social surveys, and distribution of trees. *Marine Ecology Progress Series*, **272**, pp. 77–92, 2004.
- [93] Kairo, J.G., Dahdouh-Guebas, F., Gwada, P.O., Ochieng, C. & Koedam, N., Regeneration status of mangrove forests in Mida Creek, Kenya: a compromised or secured future? *Ambio*, **31**, pp. 562–568, 2002.
- [94] Obade, P., Dahdouh-Guebas, F., Koedam, N., Wulf, R.D. & Tack, J.F., GIS-based integration of interdisciplinary ecological data to detect land-cover changes in creek mangroves at Gazi Bay, Kenya. *Western Indian Ocean Journal of Marine Science*, **3**, pp. 11–27, 2004.
- [95] Jentsch, A., Beierkuhnlein, C. & White, P.S., Scale, the dynamic stability of forest ecosystems, and persistence of biodiversity. *Silva Fennica*, **36**, pp. 393–400, 2002.
- [96] Wiegand, M.T., K.A. & Milton, S.J., Population dynamics, disturbance, and pattern evolution: identifying the fundamental scales of organization in a model ecosystem. *American Naturalist*, **152**, pp. 321–337, 1998.
- [97] Eriksson, A. & Eriksson, O., Population dynamics of the perennial *Plantago media* in semi-natural grasslands. *Journal of Vegetation Science*, **11**, pp. 245–252, 2000.
- [98] Thom, B.G., Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. *Journal of Ecology*, **55**, pp. 301–343, 1967.
- [99] Thom, B.G., Mangrove ecology - a geomorphological perspective. *Mangrove Ecosystems in Australia*, ed. B.F. Clough, Australian National University Press: Canberra, pp. 3–17, 1982.
- [100] Bugmann, H., A review of forest gap models. *Climatic Change*, **51**, pp. 259–305, 2001.
- [101] Shugart, H.H. (ed.), *A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models*, Springer-Verlag: New York, 1984.
- [102] Urban, D.L., Bonan, G.B., Smith, T.M. & Shugart, H.H., Spatial Applications of Gap Models. *Forest Ecology and Management*, **42**, pp. 95–110, 1991.