A Species-specific Individual-based Simulation Model of Mixed Mangrove Forest Stands

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Abstract: A species-specific spatially explicit individual-based model has been developed to simulate the development of mixed mangrove forest stands featuring eight species. The model is a forest stand model that forecasts mangrove forest development in a 50 m x 50 m plot by simulating the recruitment, growth, and mortality of individual mangrove trees. Species-specific growth rates, shade responses, and salinity responses of each species were incorporated to observe differences in forest structure given different salinity conditions. The model used a modified Field of Neighborhood (FON) approach that considers species-specific responses to shading and a salinity response function that considers the species-specific salinity upper boundary value of optimum growth and maximum porewater salinity of a mangrove. Simulation results of 300 years given salinity conditions in a specific site in Katunggan It Ibajay (KII) showed matching dominant species in the site. Simulation results of 500 years given extreme low and high salinity values showed consistent forest dynamics where above-ground biomass and tree count approach certain limit values as the forest stand matures. Simulation results also of 300 years given salinity values ranging from 1 – 37 ppt showed the different dominant species for different salinity conditions.

1 INTRODUCTION

The Philippines is one of the countries that hold the most diverse species of mangroves, having at least 50% of the mangrove species of the world's approximately 65 species (Garcia et al., 2013). To conserve the mangrove biodiversity in the country, several rehabilitation efforts have already been conducted in the past. Unfortunately, some have failed due to lack of knowledge on the ecology surrounding mangrove forests. To ensure that conservation efforts are successful, simulation models of mangrove forests are developed to predict the outcome of such efforts.

Mangrove forest models depict the dynamics occurring within mangrove forests. It simulates the recruitment (dispersal of seedlings), growth, and mortality (dying) of individual mangrove trees to forecast the development of the forest as a whole. Having a mangrove forest model can explain the effects of different environmental scenarios to the survival and conservation of mangrove forests.

There are several types of mangrove forest models developed. The most common type is the stand model, which simulates a mangrove forest in a relatively small area (less than 1 hectare). This type of forest model simulates different environmental conditions to analyze the effect of these conditions on the development of forests.

This paper aims to develop a model for simulating mixed mangrove forest stand dynamics. The model features a 50 m x 50 m plot where the growth of different mangrove species will be simulated given different environmental conditions. Development of the model was implemented using the AnyLogic 8.2.4 University simulation software.

Along with the development of the mangrove forest stand model, this paper also aims to conduct simulation experiments to demonstrate forest dynamics, to test species dominance at different

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salinity conditions, and to apply the model in a sample test site.

2 INTEGRATION OF CURRENT MODELS

Several mangrove forest stand models have already been developed simulating different scenarios to answer ecological questions regarding mangrove forests.

One of the most famous mangrove stand models developed is the FORMAN model (Chen and Twilley, 1998). This model is famous for featuring a mixed forest stand (a forest stand with more than one species) with mangrove species having species-specific responses to different environment factors. The FORMAN model is also a gap dynamic model, meaning it features a plot with rows and columns of cells called gaps (500 m^2 each). In the model, a tree occupies a gap but its location within the gap is not specified. Just like most mangrove stand models, each tree is described by its diameter at breast height (DBH) and height. Trees compete with other trees by the amount of light received by a tree within the gap, meaning the highest tree within the gap experiences maximum growth while the trees below experience hindered growth depending on the amount of light they receive. Trees respond to their environment based on the conditions within the gap. One of the disadvantages of this model is that the locations of trees are not explicitly defined in space; they are just defined as located in a specific gap. This makes modelling of spatially-explicit processes difficult.

This problem was addressed by the model KIWI (Berger and Hildenbrandt, 2000). In this model, the mangrove trees are explicitly defined in space, with each tree having x and y coordinates along with its DBH and height. Trees compete with each other through the Field of Neighborhood (FON) approach, where the growth of each tree is hindered by neighboring trees. The magnitude of how a tree's growth is hindered is dictated by the size, proximity, and number of neighboring trees. Trees respond to their environment by sensing the environmental conditions in their location. One of the disadvantages of this model is that light reaching an individual tree is not calculated as the FON approach already considers light availability as part of the competition computed. Hence, the species-specific responses of the mangroves to shading cannot be considered. It is important that species-specific shade-tolerance of each tree is considered as this significantly affects their growth (Dangremond et al., 2015).

Another mangrove forest model is the SEHM model (Jiang et al., 2012). The SEHM model also features a mixed stand but is composed of mangrove and hammock trees. Environment responses are not species-specific and is based on the general responses of the trees. The model aims to explain what causes the ecotones which separate the zonation of the two tree types. A unique feature of this model is its dispersal process. Unlike the other models where seedlings are placed in random locations in the plot, the SEHM model takes into account the proximity of the seedlings to its parent tree; seedlings have higher probability of being established nearer to its parent tree and a limit is set to how far seedlings can be established from the mother tree. Different types of trees have different limits of dispersal hence the species-specific dispersals of trees can be considered.

Another latest model is the mesoFON model (Grueters et al., 2014). The main feature of this model is the plasticity of each individual tree's trunk, meaning the trunk can bend in angles depending on nearby competition from other trees. A unique feature of this model is that it breaks down the Field of Neighborhood (FON) into above- and below-ground components, each signifying the competition for light and below-ground resources, respectively. This paves way to the possibility of using FON and species-specific responses to light availability at the same time.

3 STUDY AREA

The study area is the Katunggan It Ibajay (KII) Mangrove Eco-park in Aklan, Philippines. KII Eco-park was chosen because of its rich diversity of mangrove species and the availability of site data.

Data from different Philippine research projects were acquired for the simulation. Point shapefile of samples of mangrove trees in KII (Figure 1) were acquired from the Mangrove Remote Sensing (MaRS) project of the IAMBlueCECAM program. The point shapefile contains data of the species name and explicit location of the trees. Orthophoto of the area with spatial resolution of 6 cm was also acquired from the same project. Salinity raster files with spatial resolution of 10 m were acquired from the Hydrodynamic Modelling for the Assessment of Protective Services of Mangroves and Seagrass (HMAPS-MS) project of the IAMBlueCECAM program.

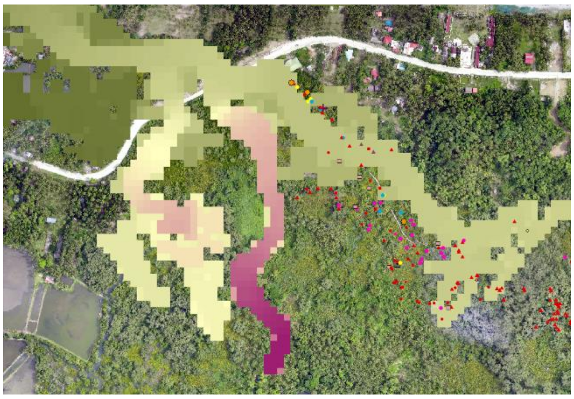


Figure 1: Orthophoto of the KII Eco-park overlayed with salinity raster file (pixels of color closer to red have lower salinity while pixels closer to green have higher salinity) and tree point shapefile (points colored based on species).

4 MANGROVE FOREST STAND MODELLING

Modelling of the mangrove forest stand was implemented through the AnyLogic 8.2.4 University simulation software. Two agents are present in the model: the Main agent which represents the environment and the Mangrove agent which represent the individual mangrove trees (Figure 2). The time step of the simulation is one year. Spatial extent was chosen to be a square plot of 50 m x 50 m to accommodate areas in the forest where the salinity data only has width of about 50 m.

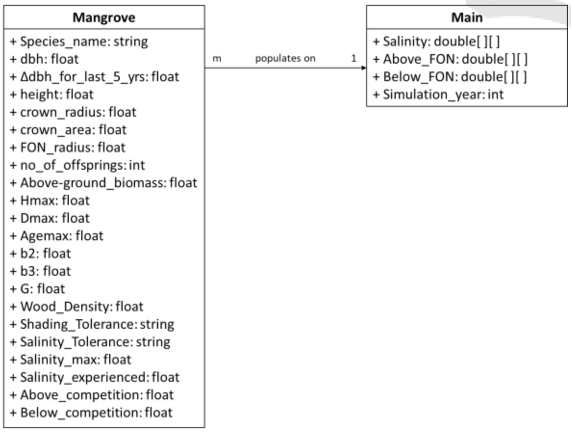


Figure 2: Class diagram of the mangrove forest stand model.

4.1 Main Agent

The Main agent, or the environment agent, holds the variables, parameters, functions, other agents, and visualization for describing the environment of the simulation. This includes the initialization, the plot, and the conditions.

For the model, the environment variables considered is salinity. Parameters accepted are the initial number of saplings and the initial conditions of the environment. Three views can be accessed in the simulation window: 2D view, 3D view, and Statistics view.

4.2 Mangrove Agent

Each mangrove agent represents an individual mangrove tree. The mangrove agent follows a statechart which describes how the agent follows the three main processes: recruitment, growth, and mortality (Figure 3).

An individual mangrove has a state of either sapling or mature. Saplings are mangrove trees that are still incapable of producing seedlings while matures can already reproduce. Transition from sapling to mature happens once the DBH of an individual tree has exceeded $1/15^{th}$ of its maximum DBH ($D > D_{max}/15$). The growth of an individual mangrove depends on its conditions such as competition from other trees and environmental factors at the site. Death occurs if the average annual growth of a tree for the last 5 years is less than half of its average growth rate ($\Delta D_{last5yrs} < 0.5*D_{max}/Age_{max}$), which happens due to aging or environmental conditions (Berger and Hildenbrandt, 2000).

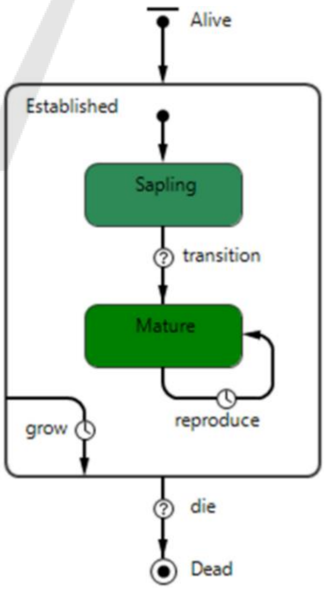


Figure 3: The statechart of the mangrove agent. Processes represented by a clock icon are executed every time step while processes represented by a question mark icon are executed only when specific conditions become true.

Table 1: Species-specific parameters for each of the eight species in the model.

	Growth							Biomass Estimation	Shading Response	Salinity Response	
Species	Form	H_{max} (cm)	D_{max} (cm)	Age_{max} (year)	b2 [7]	b3 [7]	G [7]	ρ (wood density)	Shading tolerance	Salt Tolerance	S_{max} (ppt)
Avicennia marina	Shrub [1]	1000 [2]	40 [2]	150	43.15	0.5394	63.97	0.7316 [8]	Intolerant [9]	High [11]	85 [9]
Avicennia officinalis	Tree [1]	1800 [2]	100 [2]	200	33.26	0.1663	83.34	0.6500 [8]	Intolerant [9]	High [11]	63 [9]
Nypa fruticans	Palm [1]	1000 [2]	45 [4]	100	38.36	0.4262	96.74	0.6167 [8, b]	Tolerant [10, c]	Low [11]	33 [e]
Camptostemon philippinense	Tree [1]	1000 [3]	60 [3, a]	200	28.77	0.2397	49.31	0.4867 [8]	Tolerant [9, a]	High [1, d]	75 [9, a]
Sonneratia alba	Tree [1]	1500 [3]	70 [5]	200	38.94	0.2781	70.01	0.6443 [8]	Intolerant [9]	Mid [11]	44 [9]
Xylocarpus granatum	Tree [1]	2000 [3]	80 [3]	200	46.58	0.2911	90.71	0.6721 [8]	Tolerant [9]	Low [11]	34 [9]
Ceriops decandra	Shrub [1]	500 [3]	20 [3]	150	36.30	0.9075	34.39	0.725 [8]	Tolerant [9]	Low [11]	67 [9]
Bruguiera cylindrica	Tree [1]	1500 [3]	45 [6]	200	60.58	0.6731	68.47	0.81 [8]	Tolerant [9]	Low [11]	33 [9, f]

[1] Duke et al. (1998), [2] FAO Ecocrop (2018), [3] Giesen et al. (2007), [4] CABI (2018), [5] Bojo (1995), [6] Madani and Wong (1995), [7] Botkin et al. (1972), [8] World Agroforestry (n.d.), [9] Smith (1992), [10] Ma et al. (2015), [11] Reef and Lovelock (2015),
[a] Assigned from the parameter of *Camptostemon schultzii*, [b] Assigned from the wood density of *Palma cocos Miller*, [c] Assigned from the properties of Palms in general, [d] Assigned from the estuary location of *Camptostemon schultzii*, [e] Assigned from field data, [f] Assigned from the properties of *Bruguiera sexangula*.

4.3 Gathering and Assignment of Species-specific Parameters

Eight mangrove species listed in the tree point shapefile of the study site were considered in the model (Table 1). These species have species-specific parameters which dictate their unique growth, biomass, and environmental response patterns. To assign the specific parameters of these species, different literatures were reviewed to gather the properties of these species. For the assignment of the Age_{max}, the species' form was used as basis. The Age_{max} is 100 years for palms, 150 years for shrubs, and 200 years for trees. Growth parameters b2 and b3 control the species' allometry while parameter G control the growth rate.

4.4 Growth

The model adopts the growth function for optimal conditions with reduction factor as provided in the FORMAN model (Chen and Twilley, 1998). Overall growth of a tree is represented by the yearly increase of the DBH, ΔD (cm), which is computed as follows:

$$\Delta D = \frac{G * D * \left(1 - \frac{D * H}{D_{max} * H_{max}}\right)}{274 + 3b_2 D - 4b_3 D^2} * f_{red} \tag{1}$$

where D is the tree's DBH (cm), H is the tree height (cm), and f_{red} is the reduction factor in growth due to environmental conditions. The reduction factor, which has a value range from 0 to 1, is composed of the tree's response to salinity and the combined above and below competition between trees, expressed as:

$$f_{red} = S * C \tag{2}$$

where S is the salinity response and C is the combined above and below competition response. These factors also have a value range from 0 to 1. Lower values for these factors lead to lower growth for the tree.

Tree height (cm) is computed as follows (Berger and Hildenbrandt, 2000):

$$H = 137 + b_2 D - b_3 D^2 \tag{3}$$

Crown radius (cm), r_{crown}, is computed as shown below (Berger and Hildenbrandt, 2000). The crown area (m^2), A_{crown}, is just a circle with radius r_{crown}.

$$r_{crown} = 22.2 * D^{0.654} \tag{4}$$

The Radius of Field of Neighborhood (cm), r_{FON}, is assigned as a proportion of the r_{crown}. In this model, the coefficient assigned is 1.5, as follows:

$$r_{FON} = 1.5 * r_{crown} \tag{5}$$

4.5 Recruitment

The number of saplings established in the plot per year depends on the number of seedlings produced by each tree and the environmental conditions present for the seedlings to completely turn to a sapling.

The number of seedlings, N_{seed}, produced per mangrove tree is computed as follows below (Grueters et al., 2014). The constant 0.5 was assigned so that a sufficient number of saplings are established for gaps in the forest stand.

$$N_{seed} = 0.5 * f_{red} * A_{crown} \tag{6}$$

The position of where an individual seedling will be established is randomly determined around the parent tree. The distance from the parent tree is given by the distance probability distribution, dis(d), as follows (Jiang et al., 2012):

$$dis(d) = 0.23e^{-0.2d} \tag{7}$$

where d is the distance from the parent tree. The probability of the seedling surviving to become a sapling, P_{sap}(x,y) in location (x,y) is given by the following (Berger and Hildenbrandt, 2000):

$$P_{sap}(x,y) = 1 - 2F(x,y) \tag{8}$$

where F(x,y) is the total Field of Neighborhood (FON) on the location due to competition. Once it is determined that a seedling will survive to become a sapling, a sapling will be established on the subject location with a DBH of 1.27 cm (Chen and Twilley, 1998).

This recruitment process provides stochasticity in the model and implies that different positions, number, and species of saplings are established at a certain area given different simulation runs.

4.6 Mortality

The model adopts the mortality process of the KIWI model where the probability of dying of a tree increases after continuous periods of growth depression (Berger and Hildenbrandt, 2000). Growth depression may be due to two factors: environmental stress and age.

Environmental stress may be due to exposure to harsh environmental conditions such as high salinity or low light availability due to shading. Environmental stress is signified by the reduction factor f_{red}. Growth depression due to age happens based from the growth function. As a tree reaches its maximum DBH (or maximum age), its growth decreases until the growth increment reaches 0.

When the average annual growth of a tree for its last five years, $\Delta D_{last5yrs}$, is less than half of the average annual diameter growth ($\Delta D_{last5yrs} < 0.5 * D_{max}/Age_{max}$), the tree dies and leaves the plot.

4.7 Above-ground Biomass Estimation

The above-ground biomass of an individual tree (kg), BIOM, is computed by using the biomass allometry equation that uses the wood density of a tree (Komiyama et al., 2008), as shown below. Since different species have different wood densities, different above-ground biomass will be computed for different species given the same DBH.

$$BIOM = a_{bio} * D^{b_{bio}} \tag{9}$$

4.8 Salinity Response

The salinity response, S_r, is computed using a submodel that considers the upper boundary value of optimum growth and maximum porewater salinity of a mangrove species. The submodel is given by the following:

$$S_r = \begin{cases} 1 & ; 0 \le S < S_{UOG} \\ e^{\left(-|\ln(0.1)| * \left(\frac{S - S_{UOG}}{S_{max} - S_{UOG}}\right)\right)} & ; S_{UOG} \le S < S_{max} \\ 0 & ; S_{max} \le S \end{cases} \tag{10}$$

where S_{UOG} is the assigned upper boundary salinity value for optimum growth and S_{max} is the species-specific maximum porewater salinity. S_{UOG} is assigned per species based on its Salinity Tolerance from Table 2.

Table 2: Salinity upper boundary values for optimum growth for each salinity tolerance.

Salinity Tolerance	S_{UOG}
Low	25
Mid	30
High	40

The salinity response equation was formulated so that the growth of a mangrove exponentially decays along a specific salinity gradient. At salinity values less than the S_{UOG} (or the salinity values for optimum growth), the salinity response is 1 for there is no reduction in growth. At salinity values greater than the S_{UOG}, the salinity response decreases exponentially until it becomes 0 at the salinity value of S_{max}, where the mangroves species cannot survive.

4.9 Competition between Mangrove Agents

At radius r (cm) from the center of the tree, the intensity of Field of Neighborhood (FON) exerted by a tree to signify its competition strength is given by (Berger and Hildenbrandt, 2000):

$$FON = \begin{cases} I_{max} & ; 0 \le r < r_{trunk} \\ I_{max} * e^{\left(-|\ln(I_{min})| * \left(\frac{r - r_{trunk}}{r_{FON} - r_{trunk}}\right)\right)} & ; r_{trunk} \le r \le r_{FON} \\ 0 & ; r_{FON} < r \end{cases} \tag{11}$$

where r_{trunk} is the radius of the trunk (cm) which is just half of the DBH, and I_{max} and I_{min} are competition constants (Table 3). FON was divided into above and below ground components to signify competition for light and below-ground resources availability, respectively (Grueters et al., 2014). Different I_{max} and I_{min} are used for above and below competition. The assigned I_{max} values mean that above competition (light availability) affects the growth of an individual tree significantly more than the below competition (below-ground resources availability). An I_{min} value close to 1 for below competition means that FON value is almost constant from trunk to the edge of the Field of Neigborhood. Meanwhile, an I_{min} value of 0.07 for above competitions means FON value decreases drastically at an exponential rate from trunk to the edge of the Field of Neigborhood.

Table 3: Values for I_{max} and I_{min} for above and below competition.

Competition part	I_{max}	I_{min}
Above competition	0.95	0.07
Below competition	0.05	0.999

The total competition experienced per k^{th} tree, Compet, is obtained using the following equation (Berger and Hildenbrandt, 2000):

$$Compet = \frac{1}{A_{FON}} \int_{A_{FON}} \sum_{n \neq k} FON_n(x, y) da \qquad (12)$$

This means that the sum of all FON (from neighboring trees except the tree itself) over the area within the Field of Neighborhood is the total competition. Since the FON was separated into above and below parts, the total competition also has $Compet_{above}$ and $Compet_{below}$ parts.

To obtain the competition response, the species-specific shading tolerance of the tree was considered. Equations from FORMAN (Chen and Twilley, 1998) were modified to accommodate the above competition concept. Since *Rhizophora mangle* was used in mesoFON, the shade tolerant response (the growth-reduction factor of *Rhizophora mangle* in FORMAN) is equivalent to the competition response (the growth-reduction factor used for *Rhizophora mangle* in mesoFON). The shade tolerant response, $L_{shadetolerant}$ is equated with the competition response, as given below:

$$L_{shadetolerant} = 1 - (2 * Compet_{above}) \qquad (13)$$

By rearranging the shade tolerant response equation in FORMAN, the available light, AL, is acquired as follows:

$$AL = \left(-\frac{1}{4.64} \ln(1 - L_{shadetolerant})\right) + 0.05 \qquad (14)$$

Since available light is already computed, the shade intolerant response for shade intolerant species, $L_{shadeintolerant}$ can be acquired by using the original equation from FORMAN.

$$L_{shadeintolerant} = 2.24\left(1 - e^{-1.136(AL-0.08)}\right) \qquad (15)$$

The Above Competition response, C_{above}, of a mangrove is adopted from the light responses based on the species-specific response to shade of the tree. If the mangrove species is shade tolerant, $C_{above} = L_{shadetolerant}$; if it is shade intolerant, $C_{above} = (L_{shadeintolerant} + L_{shadetolerant})/2$.

The total competition response is computed using the equation below:

$$C = C_{above} - (2 * Compet_{below}) \qquad (16)$$

5 SIMULATION EXPERIMENTS

Three simulation experiments were conducted to verify the dynamics and results of the model. For all experiments, 120 saplings, with 15 saplings per species and with DBH of 1.27 cm, were placed around the plot at the start of each simulation. Saplings were placed such that there is as much space from each other as much as possible. This initialization setting simulates an environment where a bare area is planted with saplings and as time progresses, a forest pattern with specific dominating species arises depending on the salinity condition of the area.

5.1 Validation of Site Species Dominance Experiment

The first model experiment used simulations to see if the simulation results of species dominance given actual site salinity data matches the actual species dominance in the site. For this experiment, a test site in KII which contains parts of the tree point shapefile was chosen (Figure 4). This test site, named Test Site 1, is quite upstream from the estuary but still has a high average salinity value of 25.91 ppt.

For this experiment, 10 replications of 300-year simulation runs were executed. 300 years was used as this is the forest stand age where the second generation of trees are already dominating (Bormann and Likens, 1979). The annual median total above-ground biomass (AGB) of each species for the 10 replications were acquired. Median was used instead of mean as the distribution of values of the AGB for 10 replications were not normally distributed, specifically skewed to the right.

The median AGB values from the simulations were then classified into dominance levels through the Jenks natural breaks optimization using the R programming language. The dominance level of the species at the site were also classified based on the species tree count from the shapefile. The dominance levels from the simulation and the site were then compared to see if the dominance level per species matches.

5.2 Mangrove Forest Development Experiment

The second model experiment used simulations to see how a mangrove forest stand develops as the forest stand ages. Two indicators were used to quantify the annual development of the forest stand: the total above-ground biomass (AGB) and the total tree count in the forest (N). For both indicators, only trees who have reached the mature state were considered in the calculations.

Two test sites in KII were chosen such that sites have relatively different salinity values. Test Site 2 is near the opening of the estuary in KII eco-park with average salinity value of 13.50 ppt. Test Site 3 is farther upstream from the estuary with average salinity value of 30.241.

For every site, 10 replications of 500-year simulation runs were executed. The annual mean total AGB and annual mean total tree count for the 10 replications were acquired. Annual standard deviation of the two indicators were also noted. From the values acquired, analysis was done.

Figure 4: Test sites simulated in KII Eco-park. Test Site 1 was used in the first experiment while Test Sites 2 and 3 were used in the second experiment. Test Sites 1, 2, and 3 have average salinity values of 25.91 ppt, and 30.24 ppt, 13.50 ppt, respectively.

5.3 Species Dominance Vs Salinity Experiment

The third model experiment used simulations to understand the influence of different salinity values to the dominance of mangrove species given that they were all planted as saplings at the start of simulation. Different simulation runs were executed, varying the salinity values from 1 ppt to 37 ppt with an interval of 3 ppt. 1 ppt was used as the minimum value as mangroves generally dominate in saline areas and they are outcompeted by terrestrial trees in freshwater areas. 37 ppt was used as the maximum value as 35 ppt is the average salinity value of seawater and a little leeway was given for values exceeding the average.

Per salinity value, 10 replications of 300-year simulation runs were executed. In each simulation, the subject salinity value was placed constant throughout the whole plot. After the 300^{th} year of every simulation, the dominance of each species represented by their total AGB was examined. The median total AGB for the 300^{th} year for every species for the 10 simulations was computed. The median AGB values in reference to per species and per salinity value were analyzed.

6 RESULTS AND DISCUSSION

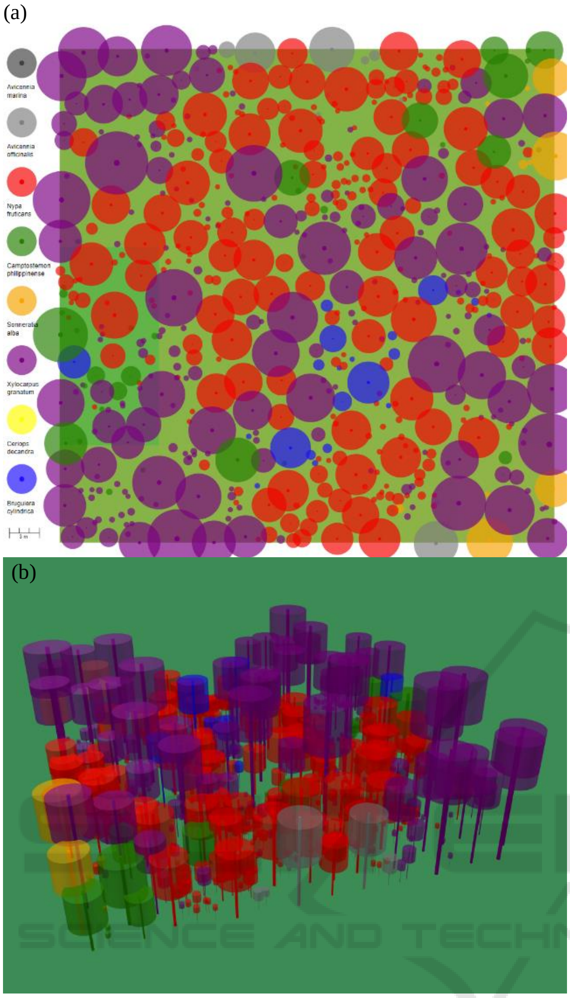
6.1 Visualization of the Mangrove Forest Stand

The visualization of the mangrove forest stand is available in 2D (POV from the sky) and 3D (Figure 5). Resulting simulation runs show that trees are spaced enough such that the canopies don’t overlap too much. Canopies of the tallest trees tend to cover almost the whole forest floor. This is in line with structures observed in forests where the tallest trees cover the forest floor, limiting the available light passing through top-most canopy. In effect, trees that are in the top-canopy are dominant in size as they don’t experience hindered growth.

Based from observation of the visualized mangrove forest stand, forest gap dynamics is followed, where saplings establish only at locations where there is available light or no above canopy. Even if a sapling was to successfully establish at locations with above canopy, it dies in about 1 or 2 years.

When a top-canopy tree dies, saplings immediately establish in the area of the deceased tree.

(a)



(b)

Figure 5: Visualization of the mangrove forest stand. (a) 2D view with POV from the sky; (b) 3D view.

This also follows the concept of gap dynamics where when a tree dies, it paves way for new trees to dominate.

6.2 Validation of Site Species Dominance

From simulation runs of Test Site 1, the dominance curves of species in relation to the forest stand age was derived (Figure 6). Throughout all years, the dominance of species with respect to each other was almost the same. *Avicennia officinalis* was the most dominating species in the mangrove forest stand. *Sonneratia alba*, *Xylocarpus granatum*, and *Camptostemon philippinensis* were also dominant but in lower numbers. *Avicennia Marina*, *Nypa fruticans*, *Ceriops decandra*, and *Bruguiera Cylindrica* were just out-dominated.

The median AGB values of the eight species at the 300th year were classified into three classes through the Jenks natural breaks optimization method using the R programming language. The three resulting classes were classified as dominance levels of High, Mid, and Low values (Table 4).

From the tree point shapefile of KII Eco-park, dominance levels of the species at the site were classified based on the number of trees that have been counted per species (Table 4). Jenks natural breaks optimization method was also used.

Comparing the dominance levels of the mangrove species in the field to the results of the simulation, six of the eight species matched, with *Avicennia officinalis* matching in high dominance, *Xylocarpus granatum* matching in mid dominance, and *Avicennia marina*, *Nypa fruticans*, *Ceriops decandra* and *Bruguiera cylindrica* matching in low dominance. The simulation results for the other two species *Camptostemon philippinense* and *Sonneratia alba*, were not far from the field data as the results were only one level different.

From the results of this experiment, the model may be ready to be used to assess the effectiveness of a mangrove reforestation effort given that the species to be used for planting and the salinity conditions in the site is known.

Table 4: Comparison of the simulated dominance level and the site dominance level per species.

Species	AGB at 300th year	Simulated dominance level	Site tree count	Site dominance level
Avicennia marina	453	Low	9	Low
Avicennia officinalis	164711	High	31	High
Nypa fruticans	916	Low	7	Low
Camptostemon philippinense	24915	Mid	6	Low
Sonneratia alba	22211	Mid	6	Low
Xylocarpus granatum	18142	Mid	20	Mid
Ceriops decandra	0	Low	3	Low
Bruguiera cylindrica	0	Low	9	Low

6.3 Mangrove Forest Development

From the simulation runs of two test sites in KII, forest development trends were observed for a 500-year period (Figure 7). As the forest stand ages, the above-ground biomass in the forest stand approaches a limit. This observation in forest dynamics is consistent with the biomass development model

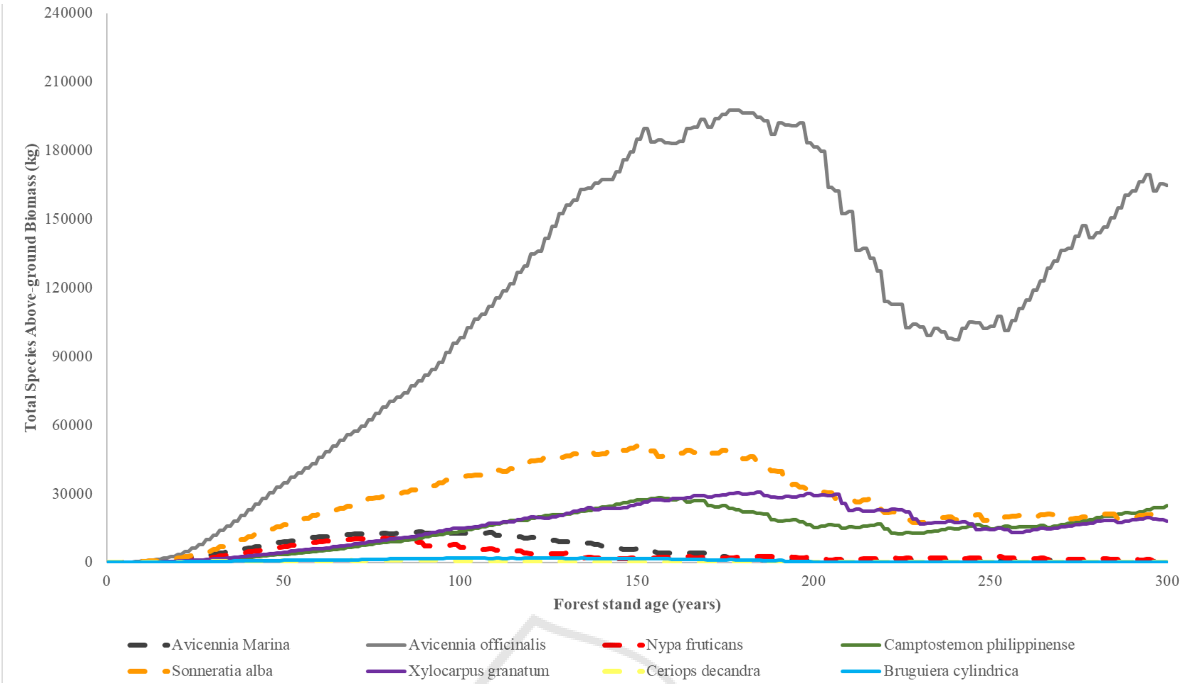


Figure 6: Dominance of eight species in KII Eco-park over a 300 year-period in Test Site 1.

Bormann and Likens, 1979; Keeton et al., 2011). In the model, it states that there will be peaks in the biomass of a forest stand in less than 200 years. In the case of the mangrove forest simulation model, the peak in biomass accumulation happens around after 150 years. The biomass development model also states that after the biomass peak, a period of a decreasing biomass happens. This is due to the dying of the first generation of mangrove trees. After this decline in biomass, a steady-state biomass is observed where the biomass of the forest approaches a certain limit. The biomass trend will increase and decrease around this limit value due to dying of dominant trees and growth of new dominant trees.

The count of individual mature trees also reaches a limit as the mangrove forest stand ages. Around the 50th year, the number of mature trees reaches a peak. After this time, individual trees start to decrease known as self-thinning due to competition between trees. During this period of self-thinning, trees start to dominate over other trees and the presence of a top-canopy becomes more evident. Around before the 200th year, mature tree count starts to increase again as the first generation of dominant trees die due to aging and saplings can now emerge now into mature trees. This is also the same period when above-ground competition for dominance. After this self-thinning period, the forest approaches a mature tree count limit. Same as the biomass, the individual tree count increase and decrease around this limit as dominant trees die and new trees grow to dominate.

The main difference of mangrove forests established at sites of different salinity values is the magnitude of values of the above-ground biomass and tree count. Mangrove forests at high salinities (Figure 7a and Figure 7b) have lower mature tree count and above-ground biomass values than mangrove forests at low salinities (Figure 7c and Figure 7d).

6.4 Species Dominance vs Salinity

From the simulation runs of different salinity conditions, the dominance curves of the eight mangrove species with respect to salinity were derived (Figure 8). For different salinity values, different mangrove species dominated the stands.

For salinity values 1 – 25 ppt, *Xylocarpus granatum* dominated over the other mangrove species. *Avicennia officinalis* and *Nypa fruticans* were second to dominate over the forest with almost biomass of the forest stand decreases. Same as the 50th year, emerging trees decrease in number due to having the same AGB values for this low salinity range. Other mangrove species were out-dominated by these species.

For salinity values greater than 25 ppt, *Avicennia officinalis* dominated the forest. Up to salinity value of 30 ppt, *Camptostemon philippinense* and

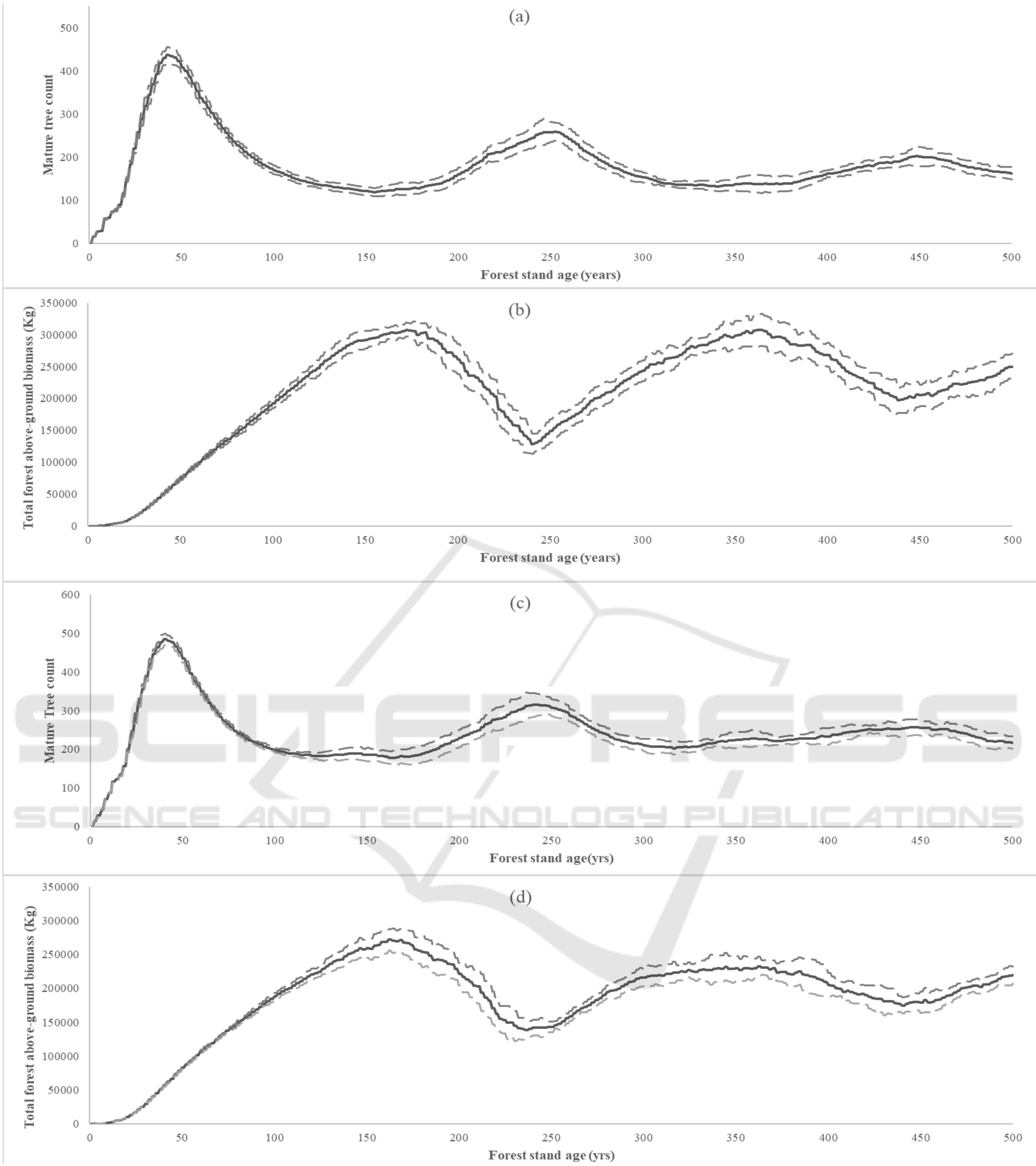


Figure 7: Trends in the development of the mangrove forest stand as it ages. Solid lines indicate the mean while the dashed lines indicate the values a standard deviation away from the mean (a) Annual mature tree count at Site 2; (b) Annual total forest AGB at Site 2; (c) Annual mature tree count at Site 3; (d) Annual total forest AGB at Site 3.

Sonneratia alba were second to dominate. At salinity values greater than 30 ppt, only *Avicennia officinalis* and *Camptostemon philippinense* have significant dominance in the forest.

It is worth noticing that the dominance of mangrove species changes drastically at around 25 ppt and 30 ppt as these values are the set upper boundaries for optimum growth for low and mid salinity tolerant

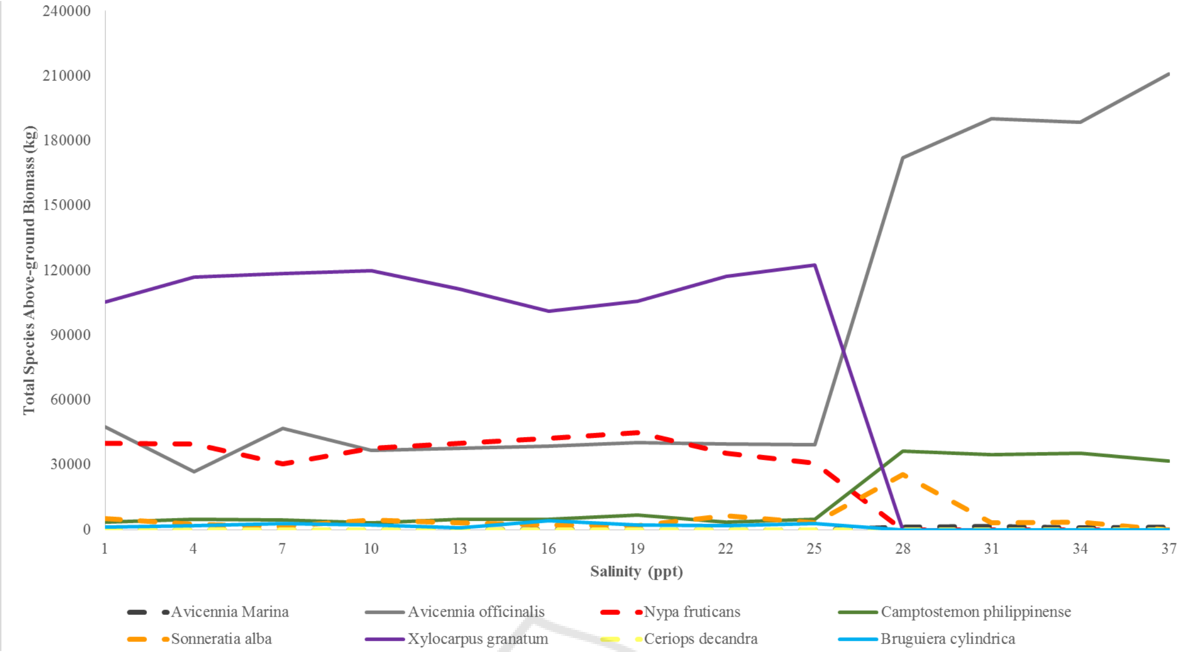


Figure 8: Dominance of eight species in KII Eco-park given different salinity conditions. Note that values of the above-ground biomass between the shown salinity values in the x-axis are interpolations, hence are approximations of simulation results for respective salinity values.

species, respectively. It is expected that adjusting these values will drastically change the species dominance curves.

Shading tolerance of each species also play a significant role in the dominance curves of the species. In the lower salinity values, *Xylocarpus granatum* dominated over the other species even if it is a low salt tolerant species. Given that the salinity conditions do not hinder the growth of the species, the shading tolerance played a vital role as *Xylocarpus granatum* can still compete with other species even in under-canopy conditions.

Lastly, the growth rates of species also play a role in the dominance curves. *Avicennia marina*, *Ceriops decandra*, and *Bruguiera cylindrica* may not be able to dominate in the forest due to a combination of either low salt and shade tolerance and low growth rates

To summarize, three factors affect the dominance curves of mangrove species: salt tolerance, shading tolerance, and the growth rate. Because of these factors, dominance curves of each species may increase and decrease through a salinity gradient. At some salinity range, a species may be more dominating as some other species may grow slow, hence it is the opportunity of the species to dominate.

7 CONCLUSION

This paper developed a model for simulating mangrove forest stand dynamics. The model simulates the development of mixed mangrove forests on a 50 m x 50 m plot given the different specific properties of each mangrove species and a set salinity condition in the site.

Results of the model simulations given the salinity conditions in a study site showed six of eight species matched actual dominance level in the site. Model simulations also displayed mangrove forest dynamics such as gap dynamics and biomass dynamics. Lastly, simulations showed the varying dominance of different mangrove species given different salinity conditions.

Given these results, the developed model is ready to be used for different applications. The model may be used for planning mangrove reforestation programs, specifically to determine if species that will be planted will be abundant given the site conditions. The model can also be used in explaining species zonation in a mangrove forest. Incorporation of more environmental factors such as inundation frequency, temperature, and biotic factors may better explain observed distribution of mangrove species in a forest. The model can also be restructured to accommodate input so that it can be used for more applications (e.g., using sea level rise data as input to assess the effect of sea level rise to the distribution of mangrove species).

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