

## FORMOSAIC: an individual-based spatially explicit model for simulating forest dynamics in landscape mosaics

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### Abstract

A forest is embedded in heterogeneous landscape mosaics and interacts with the surrounding environment through processes such as seed dispersal. Previous forest models, however, have either ignored such interactions or made unrealistic assumptions. We developed a landscape model (FORMOSAIC) that explicitly considers not only the dynamics of a focal forest but also ecological impacts of adjacent areas on the focal forest. FORMOSAIC is hierarchically structured, spatially explicit, multi-scale, stochastic, and individual-based. It integrates information of tree position, regeneration, growth, death, spatial interaction, and environmental factors. Data for parameterizing FORMOSAIC were mainly from a 50 ha permanent study plot in the Pasoh forest reserve (Malaysia), which contained over 800 tree species and more than 330 000 trees with diameter at breast height (dbh)  $\geq 1.0$  cm. Model simulation results agreed well with independent field census data in terms of species richness, species composition, tree abundance, and basal area at two spatial scales. Sensitivity analysis indicated that minimum harvest size was the most sensitive parameter. Species richness was particularly sensitive to the duration of seed immigration from species-rich surrounding forests. For tree abundance and basal area, the second most sensitive parameters varied at two spatial scales. Through uncertainty analysis we found that many parameters had scale-dependent and non-linear relationships with species richness, tree abundance, and basal area. There also existed significant interactive effects between parameters. The model could be a useful tool for addressing important issues such as fragmentation and deforestation in forest management for species diversity and timber production from a landscape perspective. © 1998 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

Biodiversity loss is accelerating because of increasing human demand for land and extensive land conversion for economic activities (Ehrlich, 1988; Wilson, 1988). The species-rich tropical forests exemplify this global phenomenon (Hubbell and Foster, 1986; Panayotou and Ashton, 1992). Deforestation and timber harvesting have likely caused many species to be extirpated from tropical forests. While establishment of nature reserves can provide refuges for some species, this traditional approach alone does not effectively conserve overall biological diversity (Hansen et al., 1991). The reasons are (1) the area of such reserves is too small and many species do not occur in the reserve; (2) it is unlikely that much more land can be set aside as reserves due to the rapid increase in human population and the subsequent demands for other uses of the land; (3) species in nature reserves could be severely affected by the changes in land use and other human activities in the surrounding landscapes.

For the reasons mentioned above, conservation of biological diversity must occur in other areas like managed forests as well as in reserves. A big challenge is to reconcile biodiversity conservation and economic goals in human-dominated ecosystems, and to link ecosystems of different levels of modification into effective and interconnected conservation networks. Management practices influence forest dynamics and successional processes by changing environmental conditions for growth, regeneration and survival. For example, timber harvesting causes varying degrees of damage to residual stands (Wyatt-Smith and Foenanter, 1962; Abdulhadi et al., 1981). Multiple objectives for the management of a single stand could result in serious conflicts, but careful design and management might lead to harmony. Adequate scientific information is essential to identify the tradeoffs (Liu et al., 1994; Pulliam and Babbitt, 1997).

Data from studies in natural forests are important for developing guidelines for managed forests (Wilcove, 1989; Hansen et al., 1991). The data require systematic analysis and synthesis for management decision making. Modeling provides a

major tool for synthesis because models can project long-term responses to changes in management practices. These models can also generate hypotheses which can be tested by experiments or field observations. A large number of forest models have been developed in the past several decades. Previous models fall roughly into two major categories: stand models and individual-based models (see numerous examples in a recent review by Liu and Ashton (1995)). Stand models are developed on information at the stand level such as tree density and total basal area (Clutter, 1963; Vanclay, 1989; Borders et al., 1990). Stand models are mainly designed for timber projection and have serious drawbacks for species diversity studies as most stand models tend to focus on timber species alone, rather than all species.

In contrast to stand models, individual-based models simulate establishment, growth, and death of each individual tree (Munro, 1974; Huston et al., 1988; DeAngelis and Gross, 1992). One way to classify individual-based models is: growth-yield and gap models (Liu and Ashton, 1995). Growth-yield models provide managers with information about growth and yield dynamics of timber trees (Monserud, 1990), while gap models are mainly used to understand forest successional patterns and processes (Shugart, 1984) in a canopy gap area created by tree falling (Botkin et al., 1972). Individual-based models have become a major approach in mimicking forest dynamics by integrating species- and size-specific information (DeAngelis and Gross, 1992).

Many studies show the importance of surrounding areas in determining ecosystem structure and function (Forman and Moore, 1992). For instance, the classic island biogeography theory of MacArthur and Wilson (1967) states that the number of species on islands is an equilibrium between immigration and extinction rates and that an island close to the mainland should support more species than an island of similar size farther from the mainland. Forest recovery in a disturbed area is inhibited due to lack of seed dispersal (Buschbacher, 1987). In tropical rain forests, many species in small forest remnants are very sensitive to the vegetation structure nearby (Lovejoy and Oren, 1981; Bierragaard et al.,

1992). However, contributions (e.g. seed dispersal) of the surrounding areas to forest dynamics have basically been ignored in previous forest models. For example, many models avoided edge effects by wrapping the modeled area onto itself (Smith and Urban, 1988), or by treating forest edges as reflecting boundaries for seeds (Clark and Ji, 1995).

Recruitment is one of the most important factors in population dynamics (Grubb, 1977). In growth-yield models for plantations, the recruitment process is usually not modeled because seedlings and saplings are generally planted (Liu and Ashton, 1995). A recent gap model by Pacala et al. (1993) assumes that all seeds are produced inside the focal area. Traditional gap models, however, introduce new individuals to a modeled area from a constant external seed pool (Botkin et al., 1972; Shugart, 1984) no matter what adjacent areas might be. This assumption warrants re-examination simply because adjacent non-forest areas (e.g. industrial or agricultural land) cannot provide any seeds to a focal forest (unless seeds are dispersed by wind from far away) and a focal forest next to a single-species plantation would be gradually dominated by the plantation species. As Clark and Ji (1995) pointed out, the sources of immigrants are critical in changing forest structure and species composition. Thus, a spatially explicit treatment of seed dispersal into a modeled forest deserves urgent attention to address management concerns such as deforestation and forest fragmentation (Harris, 1984).

In order to account for ecological processes outside a focal forest we developed a forest model (FORMOSAIC) which explicitly treats a focal forest as part of the landscape mosaics. FORMOSAIC considers not only the dynamics inside the focal area but also the impacts of adjacent areas on the focal forest. In this paper we begin with an introduction to the model structure. We then focus on methods for model parameterization and model testing by using empirical data from a long-term study site in a forest reserve of Malaysia. Finally, we present results of model testing, sensitivity analysis, and uncertainty analysis.

## 2. Methods

### 2.1. General structure of FORMOSAIC

FORMOSAIC simulates forest dynamics by integrating responses to management practices, biotic and abiotic factors which influence the recruitment, growth, and death processes (Fig. 1). Management practices may include harvesting and thinning. Biotic factors consist of intra- and inter-specific interactions (e.g. competition). Examples of abiotic factors are slope, elevation, and windthrows. Model outputs include location of each individual tree, population size of each tree species, species richness, basal area, tree density and size structure.

FORMOSAIC is hierarchically structured at four levels: landscape, focal forest, grid cell, and

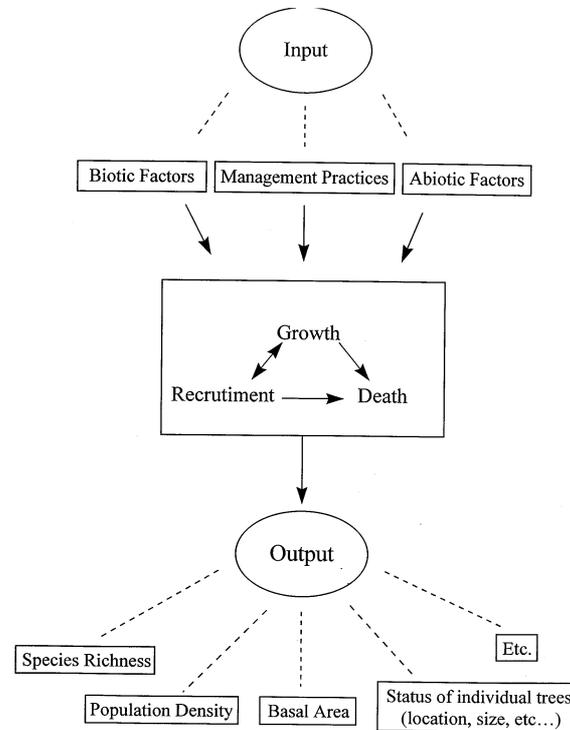


Fig. 1. Basic structure and function of FORMOSAIC. The model takes management options and other data as inputs, integrates abiotic and biotic factors which influence the death, recruitment and growth processes, and provides outputs such as species richness, basal area, and tree density.

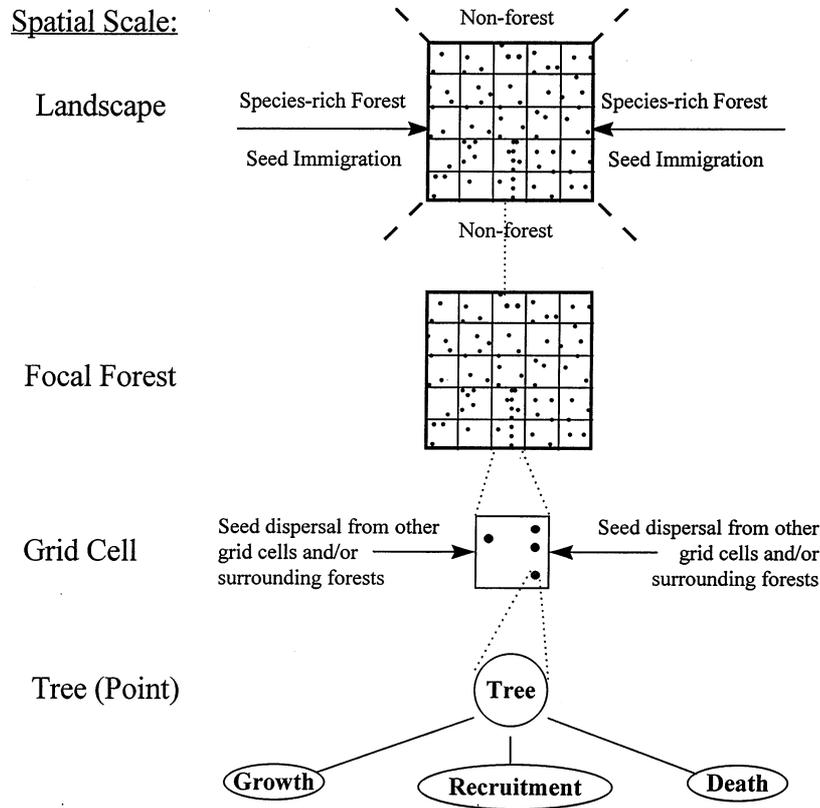


Fig. 2. Hierarchical relationship of four spatial scales (landscape, focal forest, grid cell, and tree location) considered in FORMOSAIC. At the landscape scale, this schematic diagram shows that a focal forest is surrounded by two types of adjacent areas (species-rich forest and non-forest). Seeds can immigrate into the focal forest from the adjacent species-rich forests, but no seeds are available from the neighboring non-forest. For the convenience of computation and considering ecological heterogeneity of a forest, the focal forest (0.25 ha) is represented by a grid of 25 cells. Each cell is  $10 \times 10$  m in size and contains many individuals of different tree species. Tree location is mapped at the point level. The model tracks recruitment, growth and death of each individual tree.

tree location (Fig. 2). The landscape mosaics consist of a focal forest and surrounding areas. A focal forest can be a square or rectangle in shape. The surrounding areas may be natural or plantation forests, clearcuts, agricultural fields, industrial land, roads, or residential buildings. In the current version of FORMOSAIC, surroundings are defined as the area within seed dispersal distance. In addition, the surrounding areas on the four sides (east, west, north, and south) of a focal forest may be different. For example, there may be a plantation on the west side, a natural forest on the east, a residential area on the north, and an agricultural land on the south. Fig. 2 shows a case where there are species-rich forests on the east and

west sides of a focal forest, and non-forest on the north and south sides. Seeds can immigrate into the focal forest from adjacent forests, but no seeds are available from the non-forest areas.

Considering computational efficiency and ecological heterogeneity of a forest, a focal forest is represented as a grid of  $10 \times 10$  m cells, each of which contains many individuals of different species. For example, in a 50 ha permanent plot in Malaysia (Manokaran et al., 1990), there are usually 60–80 individual trees of  $\geq 1$  cm in diameter at breast height (dbh) which belong to 30–50 tree species in a  $10 \times 10$  m area (J. Liu, unpublished data). In Fig. 2, the example focal forest is 0.25 ha in size and divided into 25 grid cells. In the model,

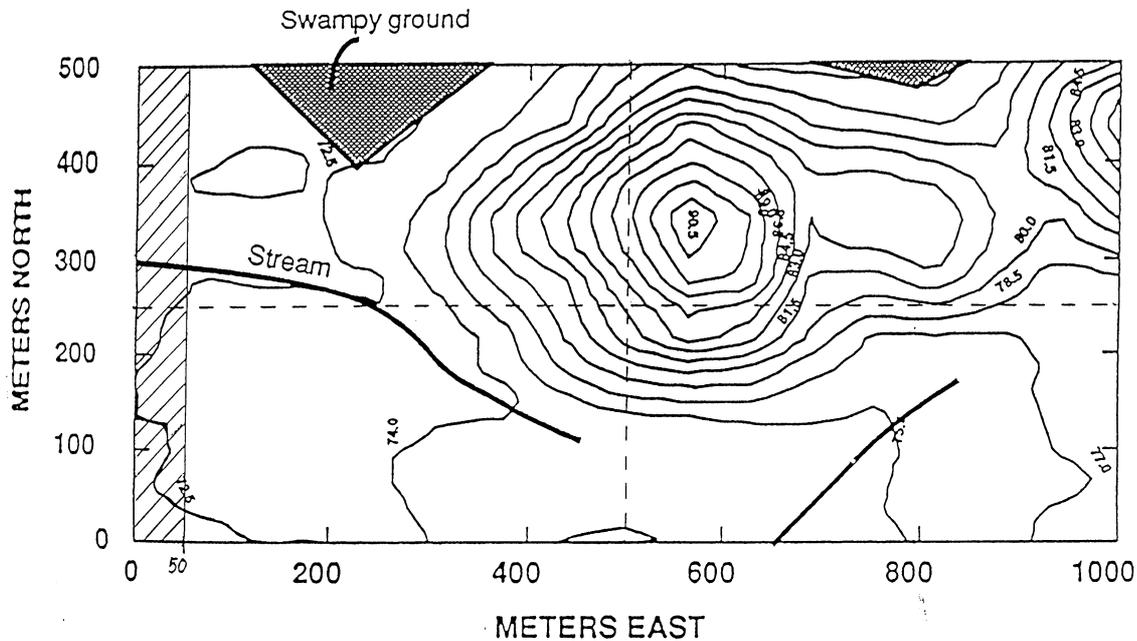


Fig. 3. Topographic map of the 50 ha long-term study plot in the Pasoh forest of Malaysia. Shading areas are swampy after wet weather. Wide solid lines represent the streams. Dashed lines divide the plot into four 12.5 ha quadrats. See text for more details.

a focal forest can be as small as a grid cell (0.01 ha), or as large as millions of hectares (depending on computer capacity). Seed dispersal can take place among grid cells. A grid cell may receive seeds produced by trees inside the cell, from other grid cells, or from outside of the focal forest. At the tree level, the location ( $x$ - and  $y$ -coordinates) of each tree is explicitly mapped. FORMOSAIC tracks recruitment, growth, and death of each individual tree.

## 2.2. Model parameterization

### 2.2.1. Data sources

The data for parameterizing FORMOSAIC were mainly from a 50 ha (500 × 1000 m) long-term study plot (Fig. 3) in the Pasoh forest reserve, Peninsula Malaysia. The plot was established in 1985 (Manokaran et al., 1990; LaFrankie, 1992a,b). It was censused in 1987 and again in 1990. At the first census the plot had over 800 tree species and more than 330 000 trees with dbh ≥ 1.0 cm. All trees were mapped and tagged, and their  $x$ - and  $y$ -coordinates were also

recorded. Demographic information included diameter growth, mortality, and recruitment. Height and crown diameter data were available from subsamples. Environmental data consisted of elevation, slope and habitat (measured as distance from swamps and streams) for each individual tree.

We designated the data from half of the plot (25 ha) for model parameterization and the other half plot for model testing. We divided the plot into 4 × 12.5 ha quadrats (Fig. 3). We chose the top right and bottom left quadrats for model development, and the top left and bottom right quadrats for model testing so that the environmental data for model development and model testing were relatively similar. Each 25 ha subplot for model development and model testing had a swamp, a stream, and a hill region (Fig. 3). While data for growth, mortality and recruitment were available throughout the 50 ha plot, we used recruitment data in only 5 ha (shading area) on the west side (Fig. 3) because the recruitment data in the other 45 ha might have too many measurement errors (J. LaFrankie, personal communica-

tion). Among the 5 ha recruitment data, we used the data in 2.5 ha for developing the recruitment submodel, and the other 2.5 ha data for model testing.

Because sample sizes in the mortality and recruitment analyses for single species were usually small, we grouped species into four guilds: emergent, canopy, understory, and successional species. The classification was based on flora information (Whitmore, 1972a,b; Ng, 1978; Swaine and Whitmore, 1988; Ng, 1989) and field knowledge of the genera including architecture, habitat, and life history (P. Ashton, observations; S. Thomas, personal communication). In the growth analysis, we also classified rare species ( $< 1$  individual  $\text{ha}^{-1}$ ) into the four guilds and developed a growth function for each guild. All species in the same guild shared the same function.

Because FORMOSAIC is individual-based, it keeps information for each individual tree (e.g. species name, size, and location) until the individual dies, and matches the species' name with guild type and uses the guild information when necessary. As a result, FORMOSAIC is able to examine species richness even though some information is guild-specific.

### 2.2.2. Growth submodel

A general growth function was developed for 502 abundant species ( $\geq 25$  individuals in total or  $\geq$  one individual  $\text{ha}^{-1}$ ) and rare species groups in the 25 ha designated for model parameterization (Eq. (1)). The relative growth is a function of dbh, neighborhood influence, slope, elevation, and the shortest distance from wet areas:

$$\begin{aligned} \ln(\text{rgr}_i) &= \beta_0 + \beta_1/\ln(\text{dbh}_i)^n + \beta_2\ln(\text{ni}_i) + \beta_3\ln(\text{slp}_i) \\ &+ \beta_4\ln(\text{ele}_i) + \beta_5\ln(\text{hab}_i) + \epsilon_i \end{aligned} \quad (1)$$

where  $\text{rgr}_i$  is the relative growth rate of individual tree  $i$ ,  $\text{dbh}_i$  is the diameter at breast height,  $n$  is a coefficient which ranged from 0.01 to 15 and differed among some species,  $\text{ni}_i$  (neighborhood influence) is the total basal area of all trees except the focal individual in a grid cell,  $\text{slp}_i$  is the slope,  $\text{ele}_i$  is the elevation,  $\text{hab}_i$  is the shortest distance from wet areas (swamp or stream), and  $\epsilon_i$  is the

error estimate. All individuals in the same species or guild of rare species shared the same equation coefficients ( $\beta_0$ – $\beta_5$ ). The means and S.E. of  $\beta_0$ – $\beta_5$  (among all abundant species and guilds of rare species) were  $-2.0092 \pm 0.5310$ ,  $1.9544 \pm 0.5279$ ,  $-0.0032 \pm 0.0005$ ,  $0.0011 \pm 0.0041$ ,  $0.0365 \pm 0.0081$ , and  $-0.0001 \pm 6.58e-5$ , respectively. Because some variables might be equal to zero in certain conditions, the value of each variable was added with 1.0 to avoid errors in arithmetic calculation. The general growth function explained up to 89% of growth variation. The average  $r^2$  across 502 abundant species was  $0.35 \pm 0.13$  (mean  $\pm$  S.E.).

We assumed that a tree would stop growing after it reaches a certain size (height or dbh). This assumption is the same as proposed in Shugart (1984). Because some variables (e.g. genetic factor) were not considered in the model, it is necessary to place a cap regarding how big a tree can grow. Otherwise, extrapolation of growth functions may result in unusually big trees. We set the maximum dbh for each species or guild of rare species at the 98th percentile of dbh distribution observed in the 25 ha subplot for model development because some extremely high dbh measurements could be errors (S. Thomas, personal communication).

### 2.2.3. Recruitment submodel

Because the number of recruits for most species in our recruitment subplot was small, we grouped all species into the four guilds as mentioned above. The minimum reproductive sizes (dbh) were set at 30.0, 20.0, 4.0 and 5.0 cm, for emergent, canopy, understory, and successional species, respectively. Size at which reproductive maturity is reached may change if a tree is in dense or 'open' forest (S. Appanah and M. Boscolo, personal communication), but there were so few studies on this that deciding on an accurate size was not easy. Therefore, we relied on findings from other study areas (Whitmore, 1972a,b; Ng, 1978, 1989). All adults in the same guild were assumed to have the same probability of reproductive success due to data limitation although variance does exist among species within the same guild (Curran et al., 1997; Davies et al., 1997).

We chose recruitment data in the 2.5 ha recruitment subplot for model development and divided the 2.5 ha subplot into 25 sections of 0.1 ha each (20 × 50 m). The recruitment rate of the emergent species did not change with tree density or basal area (Fig. 4a). Therefore, we used the average recruitment rate for the emergent species. For canopy, understory, and successional species, however, rates of recruitment decreased as the tree density increased (Fig. 4b–d). From the recruitment functions (Fig. 4) we estimated the maximum number of recruits for each guild in a grid cell (actual number of recruits might be smaller in some circumstances such as when there were no adults in the focal grid cell and/or when no immigrants came from other grid cells or outside of the forest).

Recruits in a grid cell may result from three sources: seeds immigrating from outside of a sim-

ulated forest area within dispersal distances, seeds immigrating from other cells within the simulated forest, and/or seeds produced by adults inside the focal cell (Fig. 5). We estimated the number of recruits regenerated inside a grid cell and originated from outside of a cell by considering the cell size and dispersal ability of seeds. We measured dispersal ability of seeds indirectly because we had data of new recruits instead of seeds. We used dispersal curves (numbers of recruits against distances from the parents) to describe dispersal abilities. In order to obtain dispersal curves, we needed to match recruits with their parents. When the location of a recruit was closest to an adult of the same species, we assumed that the recruit was an offspring of that adult. We realized that the accuracy of this method was not perfect, but it was the best that we could do in the absence of empirical data. Based on this parent–offspring

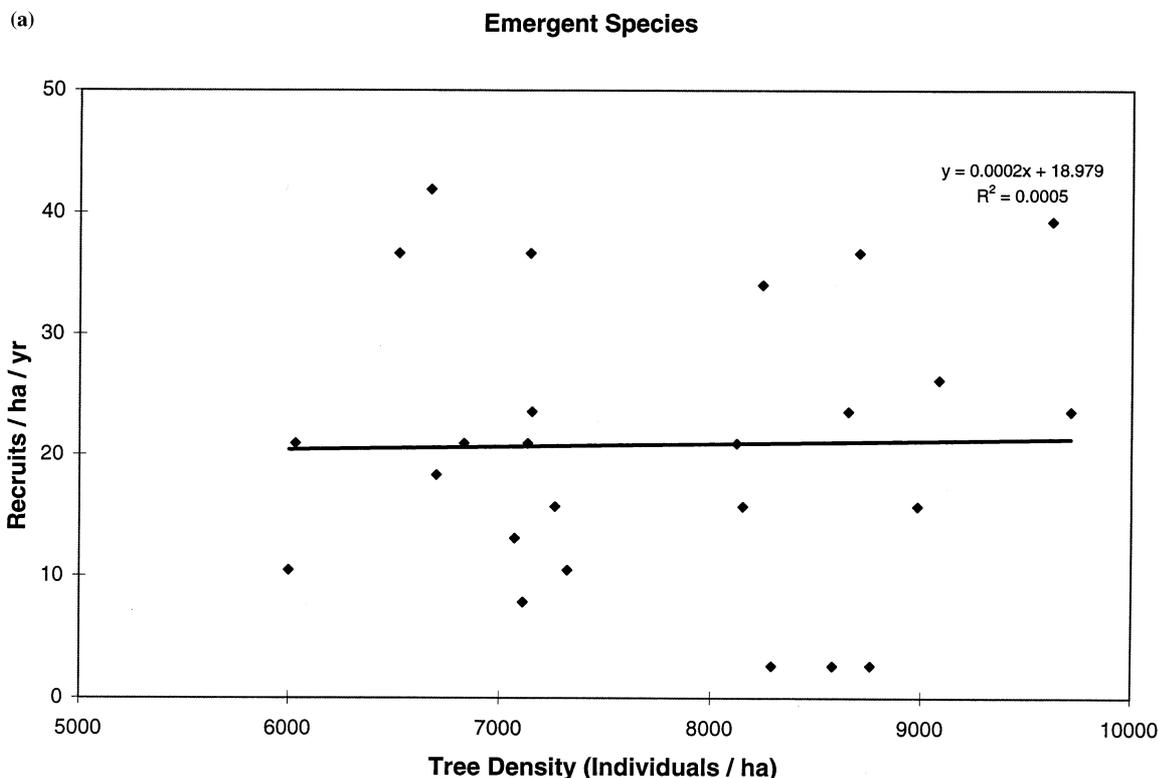


Fig. 4. Relationship between recruitment rate and tree density. Recruitment rate showed no relationship to tree density for the emergent guild (a), while recruitment rate was negatively related to tree density for canopy (b) ( $P < 0.01$ ,  $n = 25$ ), understory (c) ( $P < 0.01$ ,  $n = 25$ ), and successional species (d) ( $P < 0.05$ ,  $n = 25$ ).

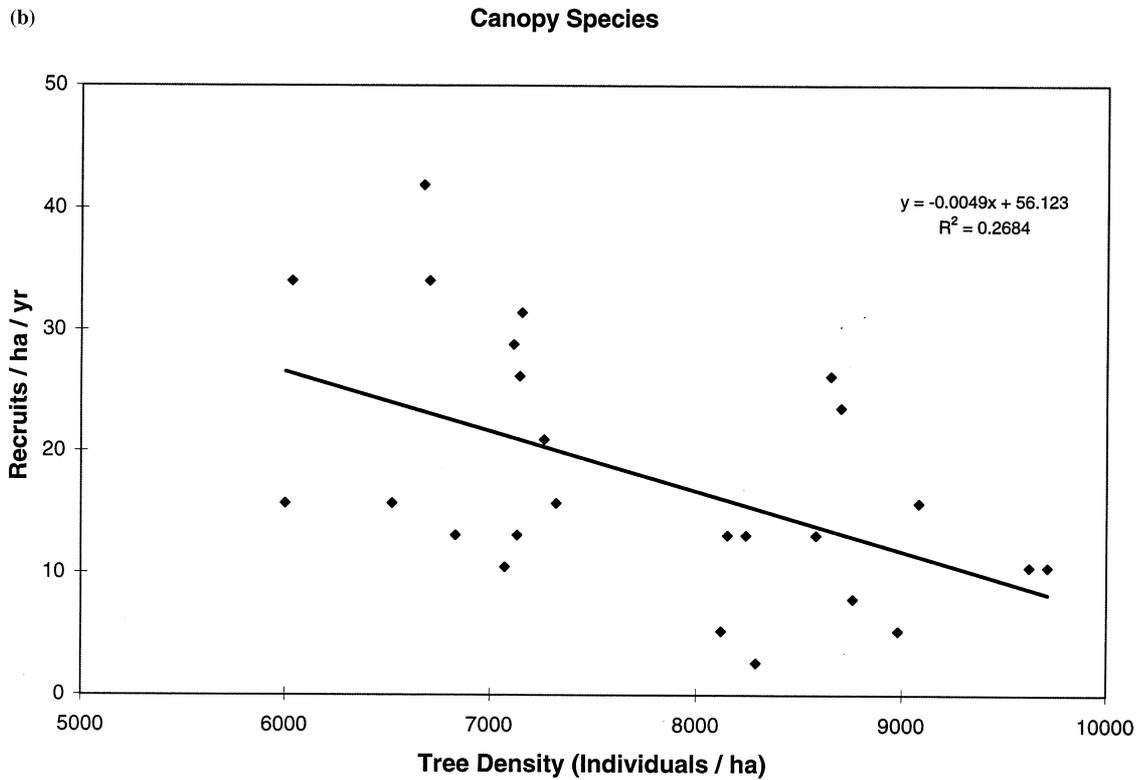


Fig. 4. (Continued)

assumption, a dispersal curve for each guild was produced (Fig. 6). When a grid cell was set to be  $10 \times 10$  m in size, percentage of recruits produced inside a grid cell ( $P_{in}$ , see below) for emergent, canopy, understory, and successional species was about 2, 2, 14, and 11%, respectively. Let the total number of recruits be  $R$  (calculated from the recruitment functions) and the proportion of recruits reproduced inside a cell be  $P_{in}$ , then the number of recruits originated from within the cell ( $R_{in}$ ) is:

$$R_{in} = P_{in} * R \quad (2a)$$

and the number of recruits from outside of the cell ( $R_{out}$ ) is:

$$R_{out} = R - R_{in} \quad (2b)$$

Immigrants (recruits originated from outside of a grid cell,  $R_{out}$ ) could come from other grid cells

within the focal forest and/or from outside of the simulated forest area. We separated these two types of sources in the following manner. We assumed that the immigrant source area (SA) was a square in shape and was delineated by the maximum dispersal distances (DD):

$$SA = (2 * DD)^2 - CL^2 \quad (3)$$

where CL is the length of the focal grid cell and  $CL^2$  is the area of the focal grid cell. The formula to calculate number of immigrants from other cells ( $I_{in}$ ) is:

$$I_{in} = (IA / SA) * R_{out} \quad (4)$$

where IA is the area of other cells within the dispersal distance from the focal cell. Thus the number of immigrants from outside of the simulated forest ( $I_{out}$ ) is:

$$I_{out} = R_{out} - I_{in} \quad (5)$$

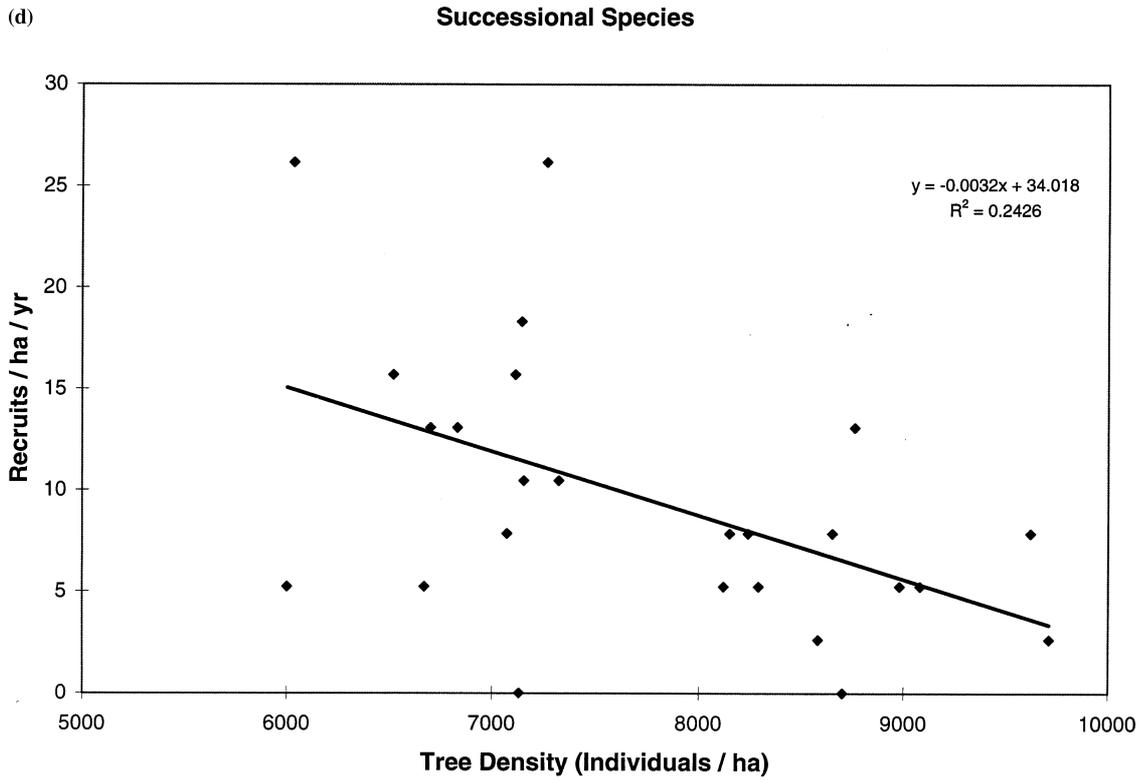
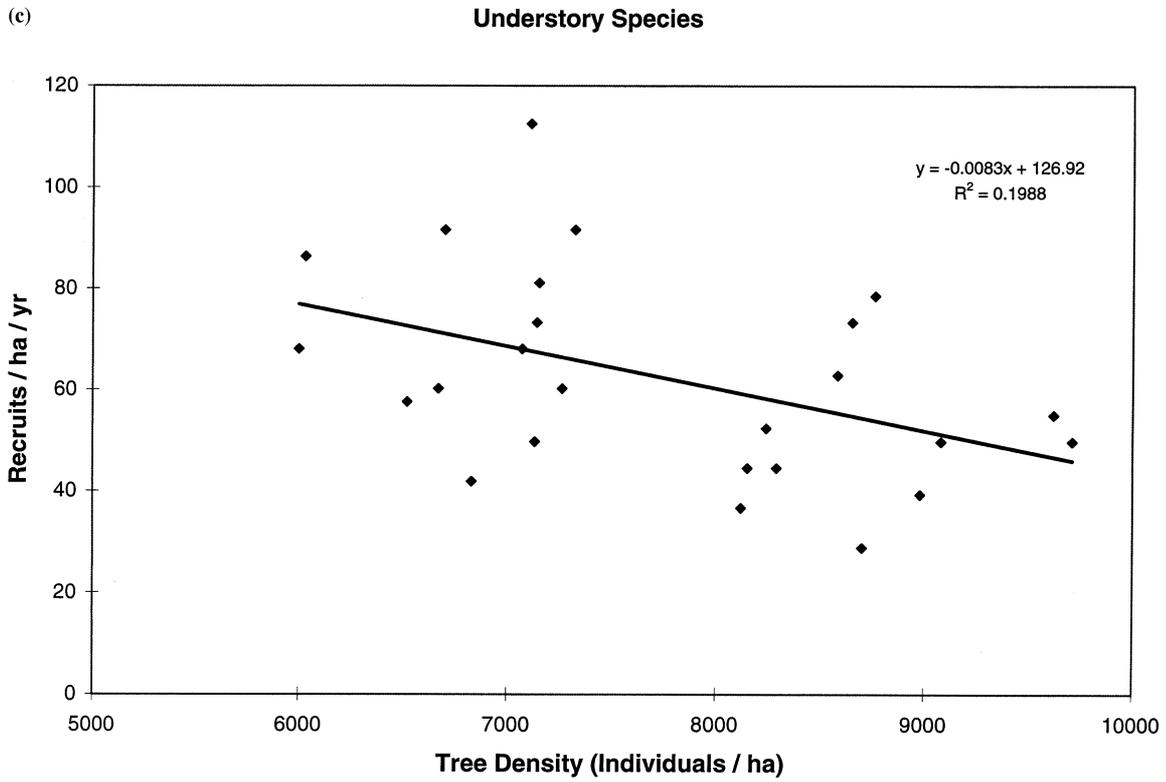


Fig. 4. (Continued)

$I_{in}$  and  $I_{out}$  change with the location of a focal cell. For example, a focal cell situated in the center of the simulated forest (Fig. 5a) has a

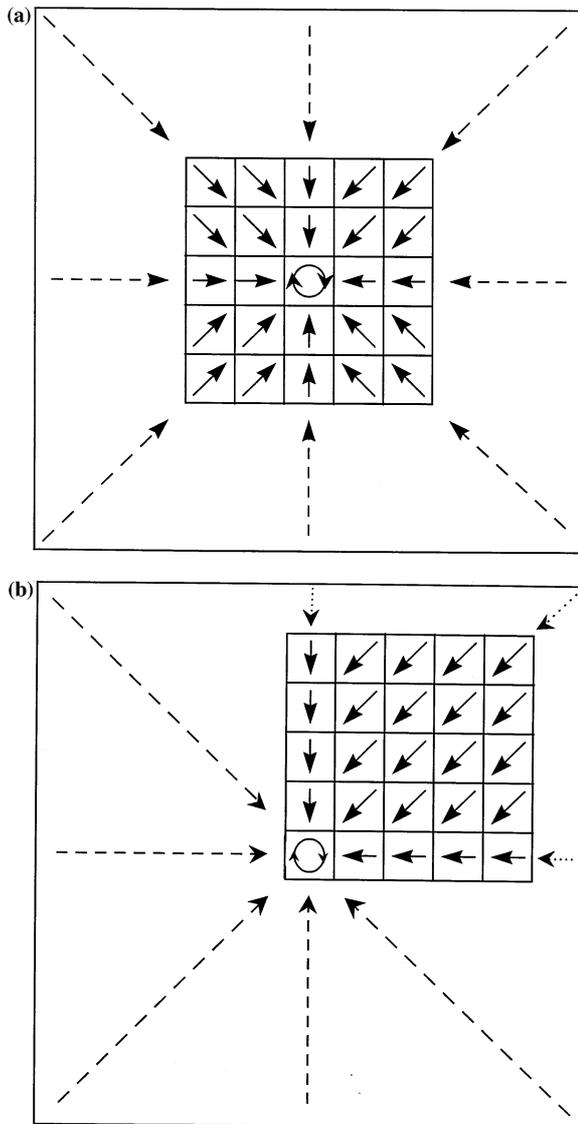


Fig. 5. Three sources of seeds which result in recruits in a grid cell: inside the grid cell (represented by cyclic arrows), from other cells (solid arrows), or from outside of the focal forest (arrows with dashed lines). Cell location is important in determining seed sources due to limited dispersal distance. A cell at the center of the focal area (a) has a lower proportion of immigrants from outside than a cell on the edge or corner (b). Furthermore, a center cell may have immigrants from all directions (a), but a corner or edge cell may not receive immigrants from all directions (b).

higher proportion of immigrants from within the focal forest than those cells near the forest boundaries.

Which species immigrate from other cells depends on the availability of seeds produced by adults in the source cells, whereas which species immigrate from outside of the forest is a function of species composition in the surrounding areas within the dispersal distances. For example, if the surrounding areas are plantations with a single species  $X$ , then the species immigrating into the focal area is  $X$ . If the surrounding areas are bare ground, there are no immigrants from outside. The model can simulate consequences of different surrounding areas by changing species composition and relative abundance of each species.

The number of potential immigrating species was determined by the number of species in the seed source area. The numbers of species in the four guilds all increased with area sizes (Fig. 7). We established the species–area relationships using data in the 25 ha subplot for model development. A species with higher population size in the source area would have a higher probability to enter the focal area. We used a stochastic process to simulate dynamic availability of recruits because there are good and bad seed years (Janzen, 1978).

As the field census only recorded recruits with  $\text{dbh} \geq 1.0$  cm, we set sizes of recruits in the model from 1.0 to 1.5 cm (dbh) at random. The location of a recruit was randomly chosen in a grid cell. Once the location was determined, the slope, elevation, and distance from wet areas were calculated for each recruit.

#### 2.2.4. Death submodel

A tree may die from chance (Botkin et al., 1972; Monserud, 1976), windthrow (Pacala et al., 1993), harvesting impact (Abdulhadi et al., 1981), or other factors including suppression due to competition (Shugart, 1984).

Annual mortality (AM) was calculated using the following equation (Sheil et al., 1995):

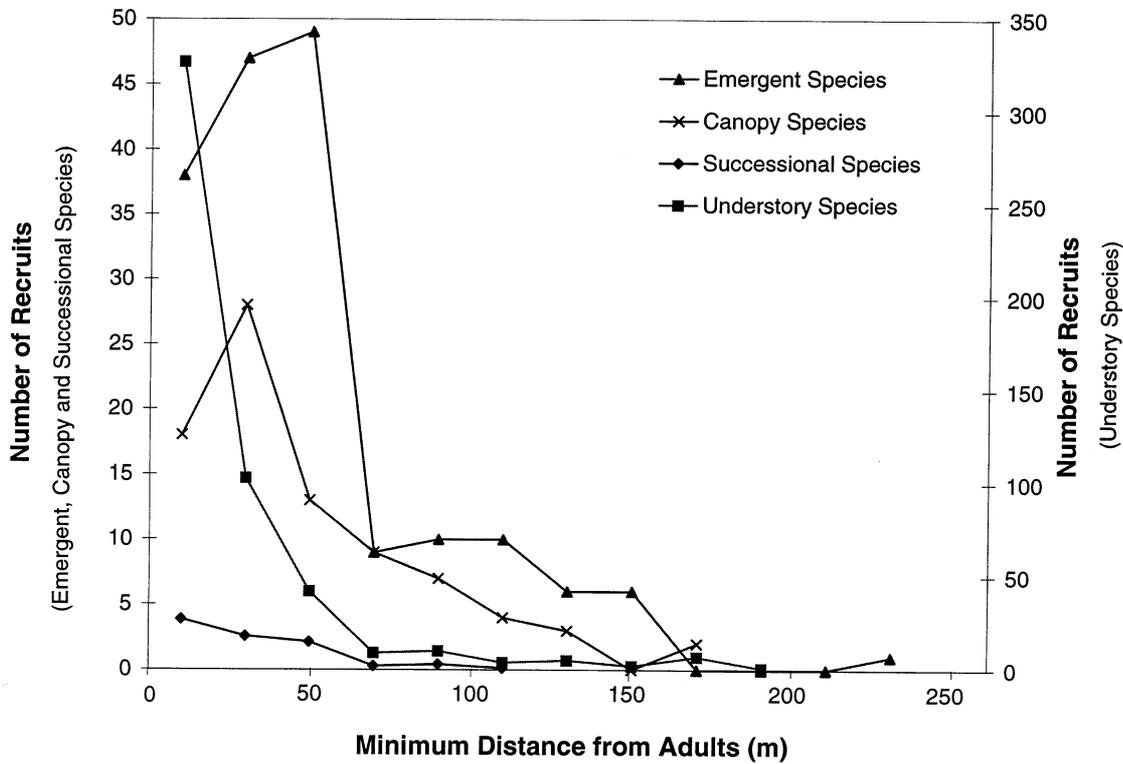


Fig. 6. Dispersal curves as depicted by the numbers of recruits against the distances from the parents for the emergent, canopy, successional, and understory species.

$$AM = 1 - \left( \frac{Nt_2}{Nt_1} \right)^{(t_2 - t_1)} \quad (6)$$

Where  $Nt_1$  is the population size at time  $t_1$ ,  $Nt_2$  is the population size at time  $t_2$ , and  $t_2 - t_1$  is the time period between two censuses. We divided the 25 ha subplot for model development into ten sections of 2.5 ha each. If the area of a section was too small, the number of dead trees would not be large enough for reasonable statistical analysis. If a section was too large, there would be too few sections for analysis.

Small trees (< 30 cm in dbh) might die of random factors and of suppression due to competition. The available data only allowed us to calculate the aggregate mortality. We divided the small trees into three size categories: 1–5, 5–10, and 10–30 cm. Except the emergent species in the 1–5 cm category and canopy species in the 10–30 cm category, all showed significant relationships between mortality and tree density or basal area.

The relationships were described by polynomial equations. The equation parameters are listed in Table 1.

Large trees ( $\geq 30$  cm in dbh) could die of aging and random factors. Because of the nature of our data set, we could not separate these two types of mortality. No significant relationships existed between the mortality and tree density or basal area. We used the average mortality across the ten sections. The four guilds had about the same probability of death (Table 1).

According to Appanah and Weinland (1993), there were 30 dipterocarp and 90 non-dipterocarp timber species in the 50 ha plot. Dipterocarps and non-dipterocarps are usually harvested at a minimum size of 50 and 45 cm, respectively (Appanah and Weinland, 1990). Harvesting not only cuts down target timber trees but also damages smaller trees nearby because of the falling of timber trees (Abdulhadi et al., 1981; Whitmore, 1984; Schaetzl

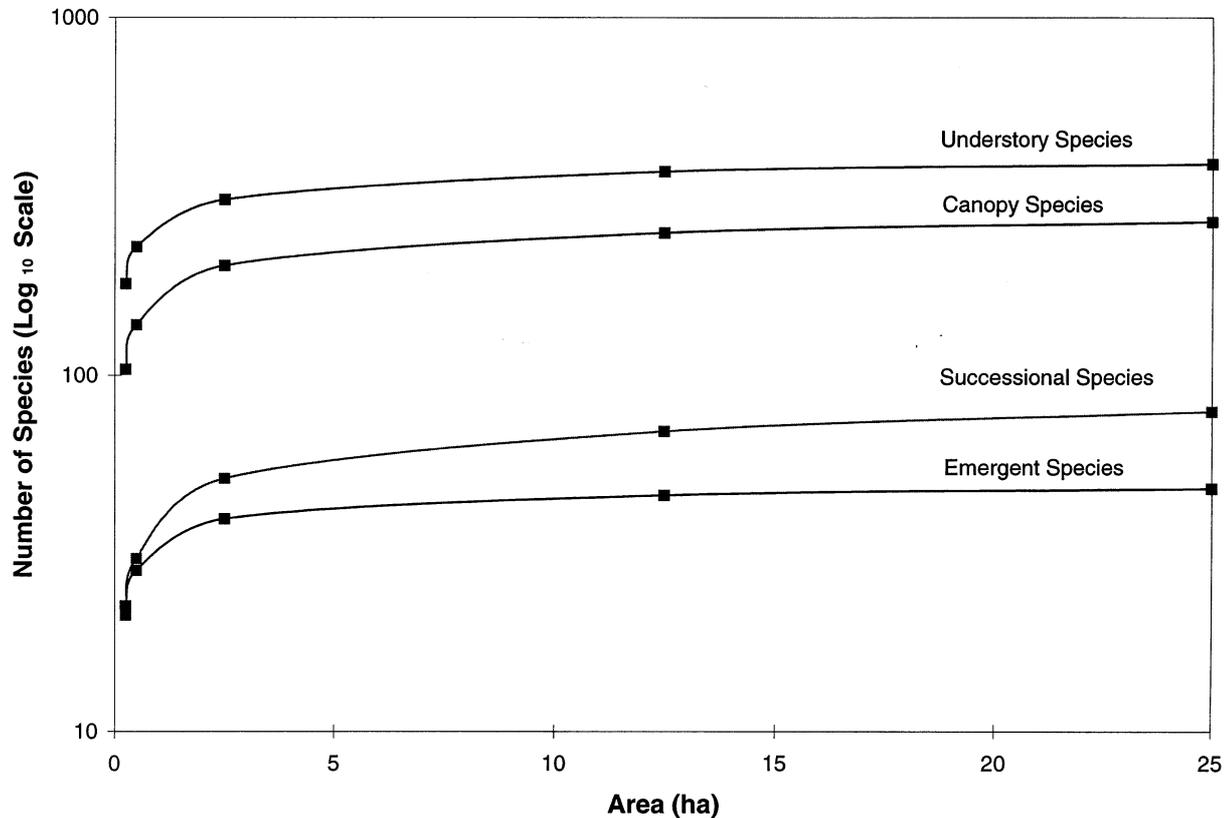


Fig. 7. The relationship between the cumulative number of species in each of the four guilds and the cumulative area.

et al., 1989; Appanah and Weinland, 1990; Vanclay, 1994). For the sake of simplicity, we assumed that a tree may fall randomly along one of the four directions (north, south, east, and west). We assumed that the damaging area (DA) or impact zone caused by a fallen tree is:

$$DA = (L * height_i) * (W * crown\_radius_i) \quad (7)$$

where  $height_i$  is the tree height (m),  $crown\_radius_i$  is the crown radius (m) of the fallen tree  $i$ ,  $L$  and  $W$  are the parameters contributing to the length and width of the damaging area, respectively (both  $L$  and  $W$  are greater than zero). Within the damage area, it is possible that only a proportion of the smaller trees ( $P$ ) would be killed. The number of smaller trees destroyed by tree falling (DS) is:

$$DS = T * P \quad (8)$$

where  $T$  is the total number of smaller trees within the damage area. Values of  $P$ ,  $L$  and/or  $W$  could be changed to simulate different degrees of logging impacts.

To measure the damage of a fallen tree to smaller trees, tree height and crown radius had to be estimated (Eq. (7)). The relationship between tree height and dbh was established from 1135 trees of seven species chosen from the 50 ha plot (Appanah, unpublished data).

$$\ln(height_i) = 0.8364 + 0.8347 \ln(dbh_i) \quad (9)$$

$(r^2 = 0.93, n = 1135)$

where  $height_i$  is the tree height (m), and  $dbh_i$  is the diameter at breast height (cm) of tree  $i$ . The equation for estimating crown radius was derived from data of 101 trees in three species of the Pasoh forest (Thomas, unpublished data).

Table 1

Coefficients of mortality function,  $y = a + bX + cX^2 + dX^3 + \varepsilon$ , where  $X$  is tree density (number of trees ha<sup>-1</sup>) or basal area (m<sup>2</sup>/ha) and  $\varepsilon$  is the error estimate

Guild	a	b	c	d	r <sup>2</sup>
<b>(A) Size class of 1–5 cm (dbh)</b>					
Emergent	0.0244	0.000	0.000	0.000	—
Canopy	1.1110	-5.013e-4	7.548e-8	-3.755e-12	0.81**
Understory	1.1382	-0.1194	4.183e-3	-4.849e-5	0.68**
Successional	2.655e+0	-2.888e-1	1.043e-2	-1.245e-4	0.73**
<b>(B) Size class of 5–10 cm (dbh)</b>					
Emergent	6.249e+0	-2.642e-3	3.712e-7	-1.729e-11	0.53*
Canopy	-3.497e+0	3.585e-1	-1.217e-2	1.372e-4	0.44*
Understory	5.090e-02	-1.501e-5	1.293e-9	0.000	0.49*
Successional	-1.003e+0	5.294e-4	-8.984e-8	4.996e-12	0.45*
<b>(C) Size class of 10–30 cm (dbh)</b>					
Emergent	1.576e+0	-6.513e-4	8.877e-8	-3.955e-12	0.47*
Canopy	0.0118	0.000	0.000	0.000	—
Understory	-1.655e+0	7.278e-4	-1.057e-7	5.113e-12	0.39*
Successional	-2.342e+1	1.026e-2	-1.490e-6	7.177e-11	0.51*
<b>(D) Size class of ≥30 cm (dbh)</b>					
Emergent	0.0114	0.000	0.000	0.000	—
Canopy	0.0098	0.000	0.000	0.000	—
Understory	0.0150	0.000	0.000	0.000	—
Successional	0.0123	0.000	0.000	0.000	—
<b>(E) Type of independent variable (X) in the mortality functions, tree size class (cm)</b>					
Guild	1–5	5–10	10–30		
Emergent	—	Tree density	Tree density		
Canopy	Tree density	Basal area	—		
Understory	Basal area	Tree density	Tree density		
Successional	Basal area	Tree density	Tree density		

The mortality functions were built for four guild types and four tree size classes.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

crown\_radius<sub>*i*</sub>

$$= 0.5 * (1.46 + 0.26 * dbh\_of\_fallen\_tree_i)$$

$$(r^2 = 0.83, n = 101) \tag{10}$$

We used Eq. (10) to represent the relationship between crown radius (m) and dbh (cm) of an individual tree *i*. The equation was applied to all species. The results might be more accurate if the information about crown–dbh relationship for every species became available. However, previous studies have shown that a vast majority of species (and all species in their young stages) demonstrate a positive linear relationship between crown radius and dbh (Krajicek et al., 1961; Dawkins, 1963; Curtin, 1964; Paudyal and Nik, 1990).

Windthrow is an important force in shaping forest dynamics (Crow, 1982; Pacala et al., 1993). Windthrow damage changes with windthrow frequency, intensity, and location as well as stand conditions such as tree height (Ruel, 1995; Mitchell, 1995). According to H.T. Chan, who is familiar with the history of the 50 ha study site (M. Boscolo, personal communication), windthrows may indeed play a significant role in the long-term dynamics of the Pasoh forest. For instance, a big windthrow occurred around 1982. However, there is little information available in regard to the frequency and intensity of windthrow damage in our study site. We assumed that a windthrow would hit a certain area in

which large trees (dbh  $\geq$  30 cm) would fall, and falling of these large trees would also damage a proportion of smaller trees within the impact zone. In FORMOSAIC, variables related to windthrows (e.g. size of impact zone, occurrence frequency and intensity) are easy to change so that windthrow effects on forest dynamics can be simulated.

### 2.2.5. Programming languages and significance tests

FORMOSAIC was programmed in an object-oriented computer programming language C++ (Ellis and Stroustrup, 1990) (see Liu (1993) for an ecological application using C++) and can be implemented in UNIX (e.g. SunSparc and Silicon Graphics workstations) and PC platforms. A friendly graphical user-interface was developed using Tcl/Tk (Welch, 1995). We employed *t*-tests and  $\chi^2$  tests (SPSS, 1996) to test for the differences between model simulation results and empirical data.

### 2.2.6. Model testing

We tested FORMOSAIC using data that were independent of model development. We divided the 2.5 ha area (0–100 m west–east, and 0–250 m south–north, with good recruitment data which were not used in parameter estimation) into ten sections of 0.25 ha each (50  $\times$  50 m). The data from the first census constituted initial species composition, structure, sizes, locations of trees in a focal area. We used species composition in the 25 ha subplot for model development as the external source of immigrants because the surrounding forest was similar to the study plot.

Each simulation had ten runs (replicates) because of stochastic processes in recruitment and mortality submodels. We ran each simulation for 4 years (each simulation step was 1 year) as the mean time between the two censuses in each section was  $> 3$  years but  $< 4$  years. In mathematical terms, the average census interval was  $3 + y$  years, where  $y$  is a decimal between 0.00 and 0.99. To assure that simulation time equals census interval, we used the following formula to weight the simulation results ( $x$ ) in each section:

$$x = \text{simulation\_result\_at\_year\_3} * (1.00 - y) + \text{simulation\_result\_at\_year\_4} * y \quad (11)$$

Where  $x$  refers to species richness, tree abundance, or basal area. We compared  $x$  with observed species richness, tree abundance or basal area from the second census.

### 2.2.7. Sensitivity and uncertainty analysis

A sensitivity analysis is used to test how a model's output responds to small changes in the parameters of interest (Jørgensen, 1986; Starfield and Bleloch, 1991; Turner et al., 1994), whereas uncertainty analysis is employed to identify how model results vary with large variances in parameters (when the parameter values have too much uncertainty or management parameters have a wide value range). Both types of analysis are useful in examining model behavior.

The sensitivity and uncertainty of parameters can be measured in several ways. For example, Turner et al. (1994) used squared Pearson correlation coefficients ( $r^2$ ) as a sensitivity and uncertainty measure under the assumption that the parameters are independent of each other. Pearson correlation coefficients are measured between each of the parameters and the model predictions. This approach is able to identify the contributions of different parameters to total variances if there are no interactions among parameters. However, the assumption of parameter independence may not always be valid, and the method cannot identify the relationship (e.g. linear or non-linear) between a dependent variable and an independent variable over a wide range of values.

In our study, we employed a simple yet widely used sensitivity index (Jørgensen, 1986):

$$S_x = (\Delta X / X) / (\Delta P / P) \quad (12)$$

where  $X$  is the dependent variable under nominal conditions,  $\Delta X$  is the difference of dependent variable between nominal conditions and modified conditions (e.g. change of value in a particular parameter),  $P$  is the parameter value under nominal conditions, and  $\Delta P$  is the difference of the

Table 2  
Parameters used for sensitivity and uncertainty analyses

Parameter ( $x$ )	Nominal value	Minimum value	Maximum value
Duration of seed immigration from surrounding species-rich forests (years)	30	0	100
Proportion of residuals damaged by harvest	0.4	0.1	0.8
Coefficient of harvest impact zone ( $L \times W$ )	1	0	4
Minimum harvest size (dbh, cm)	45	20	60
Harvest rotation (years)	30	10	40
Windthrow frequency (years)	40	0	80
Proportion of big trees damaged by windthrow	0.2	0.1	0.8
Minimum size of big trees damaged by windthrow (dbh, cm)	30	10	60
Proportion of small trees damaged by fallen big trees due to windthrow	0.2	0.1	0.8

In the sensitivity analysis, parameters were increased by 10% of their nominal value. For the uncertainty analysis, parameters were varied within the minimum and maximum values (in most cases the values were chosen at equal intervals).

particular parameter under nominal conditions and modified conditions. A larger  $S_x$  refers to a higher sensitivity of the dependent variable to a change in a particular parameter (the signs, ‘+’ and ‘-’, indicate the directions of change).

We conducted sensitivity and uncertainty analyses on nine parameters related to surrounding conditions, timber harvest and windthrow (Table 2). In the sensitivity analysis, we increased the nominal value by 10%. For uncertainty analysis, we chose a number of values within the two extremes of values of a particular parameter (Table 2), ran simulations with these values, and then did regression analysis using the simulation results. We chose linear, logarithmic, exponential, polynomial (second order), and power function to fit the curve which was formed using the dependent variable as the  $y$ -axis and the independent variable as the  $x$ -axis. The function with the lowest residuals was selected.

Like model testing, sensitivity and uncertainty analyses were done at two spatial scales (0.25 and 2.5 ha). We selected 0.25 ha (0–50 m west–east, 0–50 m south–north) or 2.5 ha area (0–100 m west–east, and 0–250 m south–north) of the 50 ha plot as a focal forest. Data for initializing simulations in sensitivity and uncertainty analyses were the same as those for model testing. Similarly, simulation step was 1 year. Each simulation run lasted 100 years and had ten replicates. We calculated the average species richness over the entire simulation period (100 years) and across replicates.

### 3. Results

Model testing at the scale of 0.25 ha demonstrated that FORMOSAIC carried out well. As can be seen in Table 3, the simulation results for species richness, tree abundance, and basal area were not significantly different from the observations ( $P = 0.46, 0.93,$  and  $0.82$  for species richness, tree abundance, and basal area, respectively). Similarly, at the scale of 2.5 ha, the simulation results did not differ from observed values in terms of species richness (Table 4,  $P = 0.16$ ), tree abundance ( $P = 0.19$ ) and basal area ( $P = 0.27$ ). The species composition from the simulations also fitted the census data very well ( $\chi^2 = 184.55$ ,  $df = 532$ ,  $P > 0.99$ ; The  $\chi^2$  value was calculated using simulated and observed population size for each species). For population sizes in 98.5% of more than 500 species, the difference between simulation and observation was not significant using  $\chi^2$  test (Fig. 8).

Sensitivity analysis indicated that at the scale of 0.25 ha, minimum size of timber trees for harvest was the most sensitive parameter for species richness, basal area, and tree abundance in a focal forest (Table 5). Species richness was also very sensitive to the duration of immigration from surrounding forests and minimum tree size felled by windthrows. The second and third most sensitive parameters for tree abundance were the proportion of smaller trees killed in the

Table 3  
Model testing results at the scale of 0.25 ha

	Observation (mean $\pm$ S.E.)	Simulation (mean $\pm$ S.E.)	<i>P</i>
Species richness (number of species/0.25 ha)	308.00 $\pm$ 3.38	311.36 $\pm$ 2.94	0.46
Tree abundance (number of trees/0.25 ha)	2111.40 $\pm$ 50.04	2117.24 $\pm$ 41.25	0.93
Basal area (m <sup>2</sup> /0.25 ha)	8.29 $\pm$ 0.52	8.14 $\pm$ 0.42	0.82

harvest impact zone and the duration of immigration (Table 5). For basal area, the two other most sensitive parameters were the proportion of smaller trees killed in the harvest impact zone and the minimum tree size felled by windthrows.

At the scale of 2.5 ha, the most sensitive parameter was still the minimum harvest size (Table 6). For species richness, the second and third most sensitive parameters remained the same (duration of immigration and minimum size of big trees felled by windthrows). For tree abundance and basal area, harvest rotation and proportion of smaller trees killed in the harvest impact zone were the second and third most sensitive parameters. Duration of immigration (the third most sensitive parameter for tree abundance at the scale of 0.25 ha) and minimum size of trees felled by windthrows (the third most sensitive parameter for basal area at the scale of 0.25 ha) were not among the three most sensitive parameters.

Uncertainty analysis at the scale of 0.25 ha showed that in many cases the relationships between species richness (or basal area, or tree abundance) and the nine parameters were non-linear (polynomial or logarithmic; Table 7). In regard to species richness, four parameters had non-linear relationships, three parameters demonstrated linear relationships, and two parameters did not display any significant relationship. As to tree abundance, three parameters showed non-linear relationships, five parameters revealed linear relationships, and one parameter had no significant relationship (Table 7). Finally, basal area exhibited a non-linear relationship with five parameters, linear relationship to three parameters, and no significant relationship with one parameter. Species richness, tree abundance and basal area all displayed the same type of relation-

ship with four of the nine parameters (duration of immigration, coefficient of harvest impact zone, minimum size of harvest, and proportion of smaller trees damaged by windthrows).

Uncertainty analysis at the scale of 2.5 ha indicated that species richness had a non-linear relationship with one parameter, linear relationships with three parameters, and no significant relationships with five parameters (Table 8). As to tree abundance, four parameters demonstrated non-linear relationships, three parameters had linear relationships, and two parameters had no significant relationship. Basal area was non-linearly related to four parameters, had a linear relationship with two parameters, and showed no relationships with three parameters (Table 8).

Results of uncertainty analysis indicated that types of relationships between species richness (or tree abundance, or basal area) and many parameters were scale-dependent. Between the two spatial scales (0.25 and 2.5 ha), five, three, and five parameters had different types of relationships with species richness, tree abundance, and basal area, respectively. For example, species richness had a non-linear relationship with proportion of residuals damaged by timber harvest at the scale of 0.25 ha but showed linear relationship at the scale of 2.5 ha.

There were apparent interactive effects of parameters on species richness, abundance, and basal area (Table 9). We used the proportion of big trees damaged by windthrow and windthrow frequency to exemplify the interactive effects at the scale of 0.25 ha. When windthrow frequency was set to 20 years, species richness linearly decreased as the windthrow damage to big trees increased. However, when windthrow frequency was 40 to 70 years, species richness did not show any relationship with the windthrow severity. Al-

Table 4  
Model testing results at the scale of 2.5 ha

	Observation	Simulation (mean $\pm$ S.E.)	<i>P</i>
Species richness (number of species/2.5 ha)	551.00	544.73 $\pm$ 3.690.16	0.16
Tree abundance (number of trees/2.5 ha)	21113.00	21053.86 $\pm$ 27.39	0.19
Basal area (m <sup>2</sup> /2.5 ha)	82.98	81.88 $\pm$ 0.47	0.27

though the relationships between tree abundance and damage to big trees were linear when windthrow occurred every 20 or 40 years, the equation coefficients were different (tree abundance was lower when windthrow frequency was 20 years). With a windthrow frequency of 70 years, the relationship between tree abundance and windthrow damage to big trees was non-linear. For basal area, it had a negative linear relationship with the proportion of big trees damaged by windthrows when windthrows occurred every 20 years. However, a lower windthrow frequency (40 or 70 years) led to a non-linear relationship between basal area and windthrow damage to big trees.

#### 4. Discussion and conclusions

FORMOSAIC was designed to simulate forest dynamics in fragmented and heterogeneous landscape mosaics, which represent a common pattern of forest distribution (Harris, 1984). Because many empirical studies indicate that forest structure and composition depend on characteristics of surrounding areas, FORMOSAIC can be a useful tool for addressing increasingly challenging issues in ecosystem management across natural and management boundaries (Christensen et al., 1996).

For a complex system like the tropical rain forest of the Pasoh forest reserve which contains over 800 tree species, it often does not have sufficient observations to establish reliable relationships for all species. Thus, a common approach is to aggregate species into groups to minimize within-group variability, with the caveat that no grouping methods are perfect. For example, Vanclay (1991) used pairwise *F*-tests to aggregate

237 species into 41 groups for developing diameter increment functions. Species in the same group shared the same growth functions. Although Vanclay's approach is automated and computationally efficient, species in the same group may differ dramatically in ecological characteristics (e.g. maximum dbh, population abundance of each species). To parameterize FORMOSAIC's mortality and regeneration submodels as well as growth submodels of rare species, we divided species into four guilds (emergent, canopy, understory and successional species) according to their ecological characteristics. For instance, all successional species tend to have high growth rates and require large gaps to regenerate. These guilds may be further divided into smaller groups to reduce within-group variations if data allow. Swaine and Whitmore (1988) suggested that further classification should be based on height at maturity. However, height at maturity may not be known for all species and may vary under different environmental conditions, and thus may not provide a good indication of growth responses critical in modeling (Vanclay, 1994).

Information for FORMOSAIC parameterization was individual-, species-, guild-, or size-specific. Variables such as neighborhood influence and the distance from wet habitats were measured for each individual tree. The growth functions for 502 abundant species were species-specific (each species had a growth function). Composition in the seed source area was also species-specific. Mortality functions, recruitment functions, and growth functions of rare species were guild-specific. All species in a guild shared the same function type and coefficients. Although FORMOSAIC performed quite well, it is still interesting to see whether refined information could further improve model performance. The data from the ongoing third census in the Pasoh

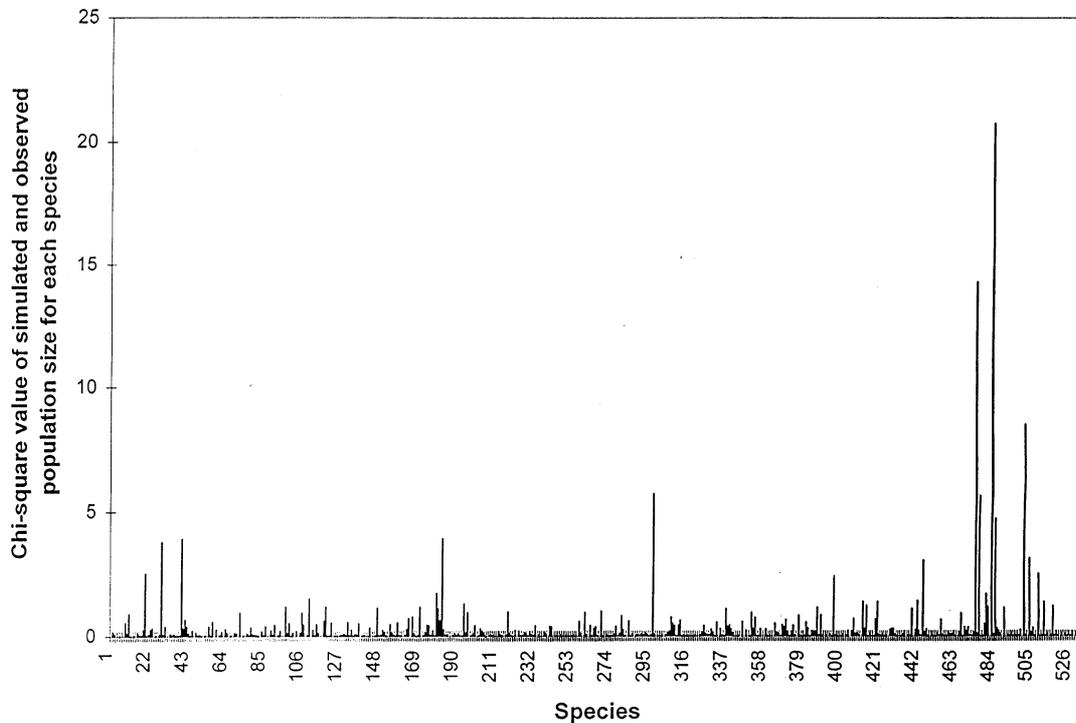


Fig. 8. Model testing in terms of species composition. Simulated and observed population sizes were not significantly different for 98.5% of more than 500 species.

Forest Reserve could be helpful for refining model parameters.

FORMOSAIC captured some essential features of a very complex rain forest, including species richness, tree abundance, basal area, and species composition. While most models were tested at a single spatial scale, FORMOSAIC was tested at two scales (0.25 and 2.5 ha). Because the data for model development and testing were relatively short-term (the time interval was about 4 years between the two censuses), long-term simulated forest dynamics should be treated as trend indicators rather than accurate prediction. The data for model development and testing were from different spatial locations (spatially independent) during the same period of time (temporally dependent). The new data from the third census in the Pasoh forest reserve will provide a useful basis to test FORMOSAIC using both spatially and temporally independent data.

Several simulation results in this study sup-

ported the intermediate disturbance hypothesis (Connell, 1979) and the island biogeography theory (MacArthur and Wilson, 1967). The intermediate disturbance hypothesis asserts that intermediate disturbance can lead to the highest species diversity. Our simulations suggested that species richness increased from a harvest rotation of 10 years, peaked when the harvest rotation was about 25 years, and then decreased as rotation lengths increased. Furthermore, our simulations also showed a positive relationship between species richness in a focal forest and the duration of seed immigration from species-rich surrounding forests. Surroundings of a focal forest may be similar to the 'mainland' in the island biogeography theory, whereas the focal forest may be equivalent to an 'island'. Species richness on an 'island' depends upon a supply of immigrants from the 'mainland'.

Through sensitivity and uncertainty analyses, we were able to identify the responses of species

Table 5  
Sensitivity index at the scale of 0.25 ha

Parameter ( $x$ )	Species richness	Tree abundance	Basal area
Duration of seed immigration from surrounding species-rich forests (years)	0.17	0.21	−0.25
Proportion of residuals damaged by harvest	−0.07	−0.30	−0.91
Coefficient of harvest impact zone	0.07	−0.05	−0.30
Minimum harvest size (dbh, cm)	0.31	0.56	1.33
Harvest rotation (years)	−0.04	0.04	−0.24
Windthrow frequency (years)	0.07	0.01	−0.05
Proportion of big trees damaged by windthrow	0.05	0.05	−0.10
Minimum size of big trees damaged by windthrow (dbh, cm)	0.09	−0.02	−0.49
Proportion of small trees damaged by fallen big trees due to windthrow	0.03	−0.05	−0.24

Table 6  
Sensitivity index at the scale of 2.5 ha

Parameter ( $x$ )	Species richness	Tree abundance	Basal area
Duration of seed immigration from surrounding species-rich forests (years)	0.10	0.13	0.05
Proportion of residuals damaged by harvest	−0.07	−0.27	−0.37
Coefficient of harvest impact zone	−0.04	0.09	0.23
Minimum harvest size (dbh, cm)	0.21	0.76	1.57
Harvest rotation (years)	−0.05	−0.64	−1.45
Windthrow frequency (years)	−0.05	−0.01	0.05
Proportion of big trees damaged by windthrow	0.10	−0.02	−0.04
Minimum size of big trees damaged by windthrow (dbh, cm)	−0.08	−0.06	−0.18
Proportion of small trees damaged by fallen big trees due to windthrow	−0.03	0.06	0.09

richness, tree abundance, and basal area to changes in some of FORMOSAIC's parameters. Impacts of many parameters were scale-dependent and non-linear, which are consistent with some previous work (Levin, 1992; Turner et al., 1995). We also observed interesting interactive effects between parameters through a case study on windthrow frequency and windthrow damage to big trees (Table 9). In this study, we only considered the interactions between windthrow frequency and the proportion of big trees damaged by windthrows, further research is warranted to explore the interactive effects among other parameters.

FORMOSAIC is an individual-based and spatially explicit model. As such it shares some features with other individual-based and spatial forest models (e.g. tracking behavior of each individual tree) (Urban, 1990; Pacala et al., 1993). However, FORMOSAIC also differs from a typical gap model (Botkin et al., 1972; Shugart, 1984) in the following four major aspects. First,

it considers the impacts (seed immigration) from the surroundings explicitly whereas a typical gap model does not. In FORMOSAIC, recruits can be regenerated from seeds of three possible origins: inside a basic spatial unit (grid cell) of the focal forest, from other cells within the focal forest, and from the surrounding forests. Second, FORMOSAIC simulates the dynamics of an entire forest (which may consist of both gaps and non-gaps at the same time) whereas a typical gap model simulates the dynamics of a gap only. Third, the functions for growth, mortality, and recruitment in FORMOSAIC are derived from demographic census data whereas a typical gap model has light and moisture-driven functions that include detailed vertical layers through the canopy. Growth functions of many species in FORMOSAIC have slope, elevation and distance as independent variables in addition to tree size and neighborhood pressure. Thus individuals of the same species may be in different conditions and therefore may have different gr-

Table 7  
Relationship between species richness (or tree abundance, or basal area) and each of the parameters (uncertainty analysis at the scale of 0.25 ha)

Parameter (x)	Species richness		Tree abundance		Basal area	
	n	Equation	r <sup>2</sup>	Equation	r <sup>2</sup>	Equation
Duration of immigration	5	0.7455x+241.54	0.96**	2.5578x+1697	0.99**	-0.0075x+11.612
Proportion of residuals damaged due to harvest	6	-27.839x <sup>2</sup> +6.9592x+311.48	0.82**	-441.92x+2132.7	0.96**	-4.6398x+12.782
Coefficient of harvest impact zone	5	-2.7663x+312.93	0.95**	-71.261x+2078	0.82*	-0.7506x+12.145
Minimum harvest size	6	23.607 ln(x)+218.61	0.85**	416.9 ln(x)+314.35	0.94**	5.068 ln(x)-9.093
Harvest rotation	5	-0.0201x <sup>2</sup> +1.0048x+299.51	0.99**	-0.0648x <sup>2</sup> +3.6359x+1903.8	0.49 <sup>NS</sup>	-0.001x <sup>2</sup> +0.0539x+10.217
Windthrow frequency	6	0.0016x <sup>2</sup> -0.108x+310.84	0.26 <sup>NS</sup>	0.0308x <sup>2</sup> -2.2549x+1976.6	0.41 <sup>NS</sup>	0.0007x <sup>2</sup> -0.05x+11.478
Proportion of big trees damaged by windthrow	6	-7.8955x <sup>2</sup> +6.3371x+308.47	0.18 <sup>NS</sup>	-92.898x+1976.3	0.91**	-0.5992ln(x)+9.9885
Minimum size of big trees damaged by windthrow	6	-7.8402x+311.74	0.58**	-201.56x <sup>2</sup> +72.801x+1959.7	0.78**	-1.1126x <sup>2</sup> +0.0392x+11.061
Proportion of small trees damaged by fallen big trees due to windthrow	7	-0.0087x <sup>2</sup> +0.7081x+296.48	0.90**	0.0219x <sup>2</sup> +0.2725x+1901.8	0.40 <sup>NS</sup>	0.0001x <sup>2</sup> +0.0136x+10.28

NS, not significant.  
\* P < 0.05.  
\*\*\* P < 0.01.

Table 8  
Relationship between species richness (or tree abundance, or basal area) and each of the parameters (uncertainty analysis at the scale of 2.5 ha)

Parameter (x)	Species richness		Tree abundance		Basal area	
	n	Equation	r <sup>2</sup>	Equation	r <sup>2</sup>	Equation
Duration of immigration	5	0.4782x + 476.8	0.89**	16.797x + 16188	0.98**	-0.0171x + 96.178
Proportion of residuals damaged due to harvest	6	-42.59x + 534.53	0.94**	-5300.7x + 20063	0.99**	-48.33x + 114.22
Coefficient of harvest impact zone	5	-11.711x + 532.67	0.99**	290.07x <sup>2</sup> - 2455.2x + 20285	0.97***	2.2875x <sup>2</sup> - 20.483x + 114.84
Minimum harvest size	6	47.269 ln(x) + 336.77	0.96**	5063.9ln(x) - 1892	0.97**	49.986 ln(x) - 100.88
Harvest rotation	5	-0.0045x <sup>2</sup> + 0.1749x + 516.52	0.08 <sup>NS</sup>	-0.1614x <sup>2</sup> + 11.232x + 17570	0.12 <sup>NS</sup>	-0.0021 x <sup>2</sup> + 0.145x + 91.034
Windthrow frequency	6	0.0003x <sup>2</sup> - 0.0158x + 518.93	0.01 <sup>NS</sup>	0.1318x <sup>2</sup> - 12.015x + 18049	0.32 <sup>NS</sup>	0.0022x <sup>2</sup> - 0.1743x + 96.44
Proportion of big trees damaged by windthrow	6	22.037x <sup>2</sup> - 26.74x + 522.26	0.42 <sup>NS</sup>	1057.8x <sup>2</sup> - 1872.8x + 18101	0.82**	-11.957x + 95.776
Minimum size of big trees damaged by windthrow	6	-13.093x <sup>2</sup> + 4.3905x + 518.6	0.37 <sup>NS</sup>	-1878.9x <sup>2</sup> + 675.3x + 17788	0.85**	-21.914x <sup>2</sup> + 10.782x + 92.86
Proportion of small trees damaged by fallen big trees due to windthrow	7	-0.0053x <sup>2</sup> + 0.4717x + 509.01	0.47 <sup>NS</sup>	-1.2975x <sup>2</sup> + 117.72x + 15467	0.96**	-0.0109x <sup>2</sup> + 1.0461x + 72.3

NS, not significant.  
\*\* P < 0.01.

Table 9  
Interactive effects between windthrow frequency and proportion of big trees damaged by windthrow

Windthrow frequency (years)	Species richness		Tree abundance		Basal area	
	Equation	$r^2$	Equation	$r^2$	Equation	$r^2$
20	$-4.276x + 309.95$	0.66*	$-155.63x + 1973.5$	0.98**	$-2.4063x + 11.142$	0.97**
40	$-7.8455x^2 + 6.3371x + 308.47$	0.18 <sup>NS</sup>	$-92.898x + 1976.3$	0.91**	$-0.5992\ln(x) + 9.9885$	0.82**
70	$-6.857x^2 + 9.9925x + 305.86$	0.45 <sup>NS</sup>	$-63.429x^2 + 1.6595x + 1959.4$	0.86**	$-1.754x^2 + 0.7826x + 10.922$	0.81**

\*\*  $P < 0.01$ .

\*  $P < 0.05$ .

rowth rates. Fourth, FORMOSAIC considers horizontal differences (e.g. location) among trees even within the same grid cell while a typical gap model does not.

FORMOSAIC was developed as a first attempt to explicitly address the interactions among adjacent areas, focal forest, and natural and anthropological disturbances. Although room exists for improving and refining FORMOSAIC, we believe that our new approach provides a prototype for simulating forest dynamics and for evaluating management consequences across different boundaries (e.g. natural, ownership, and management). Because various forest types share many similarities (e.g. fragmentation as in Harris (1984)), the modeling paradigm presented in this paper can also be useful for understanding and managing forest dynamics from a landscape perspective in temperate and boreal forest zones as well as tropical regions.

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### References

- Abdulhadi, R., Kartawinata, K., Sukardjo, S., 1981. Effects of mechanized logging in the lowland dipterocarp forest at Lempake, East Kalimantan. *Malays. For.* 44, 407–418.

- Appanah, S., Weinland, G., 1990. Will the management systems for hill dipterocarp forest stand up? *J. Trop. For. Sci.* 3, 140–158.
- Appanah, S., Weinland, G., 1993. A Preliminary Analysis of the 50-hectare Pasoh Demography Plot: I. Dipterocarpaceae. Forest Research Institute Malaysia, Kepong, Malaysia.
- Bierragaard Jr., Richard O., Lovejoy, Thomas E., Kapos, Valerie, Angelo Augusto dos Santos, Hutchings, Roger W., 1992. The biological dynamics of tropical rainforest fragments. *BioScience* 42, 859–66.
- Borders, B.E., Harrison, W.M., Adams, D.E., Bailey, R.L., Pienaar, L.V., 1990. Yield prediction and growth projection for site prepared loblolly pine plantations in the Carolinas, Georgia, and Alabama, Research Paper 1990–2. School of Forest Resources, University of Georgia, Athens, GA.
- Botkin, D.B., Janak, J.S., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60, 167–179.
- Buschbacher, R.J., 1987. Deforestation for sovereignty over remote frontiers. In: Jordan, C.F. (Ed.), *Amazonian Rain Forests: Ecosystem Disturbance and Recovery*. Spinger, NY, pp. 46–57.
- Christensen, Norman L., Bartuska, Ann M., Brown, James H., et al, 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecol. Appl.* 6, 665–91.
- Clark, J.S., Ji, Y., 1995. Fecundity and dispersal in plant populations: Implications for structure and diversity. *Am. Nat.* 146, 72–111.
- Clutter, J.L., 1963. Compatible growth and yield models. *For. Sci.* 9, 354–371.
- Connell, J.H., 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. In: Anderson, R.M., Turner, B.D., Taylor, R.D. (Eds.), *Population Dynamics*. Blackwell, Oxford, pp. 141–163.
- Crow, T.R., 1982. A rainforest chronicle: a 30-year record in structure and composition at El Verde, Puerto Rico. *Biotropica* 12, 42–55.
- Curran, L.M., Leighton, M., Kusneti, M., 1997. Temporal and Spatial Distribution of Fruitfall in Mast-Fruiting Bornean Dipterocarpaceae: II. Seed Production, Predator-Satiation, Pre-Dispersal Predation, and Its Effects on Recruitment Limitation. *J. Ecol.* (in review).
- Curtin, R.A., 1964. Stand density and the relationship of crown width to diameter and height in *Eucalyptus Obliqua*. *Aust. For.* 29, 91–104.
- Dawkins, H.C., 1963. Crown diameters: their relation to bole diameter in tropical forest trees. *Commonw. For. Rev.* 42, 318–333.
- Davies, S.P., Ashton, P.S., Lee, H.S., 1997. Life History Diversity in Tropical Pioneer Trees: Comparative Demography and Allometry of Eleven Species of Macaranga from Borneo. *J. Ecol.* (in press).
- DeAngelis, D.L., Gross, L.J., 1992. Individual-based models and approaches in ecology: Populations, communities and ecosystems. In: DeAngelis, D.L., Gross, L.J. (Eds.), Chapman and Hall, NY.
- Ehrlich, P.R., 1988. The loss of diversity: Cause and consequences. In: Wilson, E.O. (Ed.), *Biodiversity*. National Academy Press, Washington, DC, pp. 21–27.
- Ellis, M.A., Stroustrup, B., 1990. *The Annotated C++ Reference Manual*. Addison-Wesley Publishing Company, Reading, Massachusetts.
- Forman, R.T.T., Moore, P.N., 1992. Theoretical foundations for understanding of boundaries in landscape mosaics. In: Hansen, A.J., diCasteri, F. (Eds.), *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer, NY, pp. 236–258.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107–145.
- Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests: lessons from natural forests. *BioScience* 41, 382–392.
- Harris, L.D., 1984. *The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity*. University of Chicago Press, IL.
- Hubbell, S.P., Foster, R.B., 1986. Commonness and rarity in a neotropical forest: Implications for tropical tree conservation. In: Soule, Michael E. (Ed.), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, MA, pp. 205–231.
- Huston, M., DeAngelis, D., Post, W., 1988. New computer models unify ecological theory. *BioScience* 38, 682–691.
- Janzen, D.H., 1978. Seeding patterns of tropical trees. In: Tomlinson, P.B., Zimmermann, M.H. (Eds.), *Tropical Trees as Living Systems*. Cambridge University Press, London, pp. 83–128.
- Jørgensen, S.E., 1986. *Fundamentals of Ecological Modelling*. Elsevier, Amsterdam.
- Krajicek, J.E., Brinkman, K.A., Gingrich, S.F., 1961. Crown competition—A measure of density. *For. Sci.* 7, 35–42.
- LaFrankie, J.V., 1992a. The 1992 data set for the Pasoh 50 ha forest dynamics plot. Miscellaneous Internal Report 26.9.92. Center For Tropical Forest Science, Smithsonian Institute for Tropical Research.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- LaFrankie, J.V., 1992b. Estimating diameter growth from the 50 ha permanent plot data set at Pasoh Forest Reserve, Malaysia. Miscellaneous Internal Report 26.8.92. Center For Tropical Forest Science, Smithsonian Institute for Tropical Research.
- Liu, J., 1993. ECOLECON: An ECOLOGical-ECONomic model for species conservation in complex forest landscapes. *Ecol. Model.* 70, 63–87.
- Liu, J., Cabbage, F.W., Pulliam, H.R., 1994. Ecological and economic effects of forest landscape structure and rotation length: simulation studies using ECOLECON. *Ecol. Econ.* 10, 249–263.
- Liu, J., Ashton, P.S., 1995. Individual-based simulation models for forest succession and management. *For. Ecol. Manag.* 75, 157–175.

- Lovejoy, T.E., Oren, D.C., 1981. Minimum critical size of ecosystems. In: Burgess, R.L., Sharp, D.M. (Eds.), *Forest Island Dynamics in Man-dominated Landscapes*. Springer, New York, pp. 7–12.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Manokaran, N., LaFrankie, J.V., Kochummen, K.M., Quah, E.S., Klahn, J.E., Ashton, P.S., Hubbell, S.P., 1990. Methodology for the Fifty Hectare Research Plot at Pasoh Forest Reserve, Research Pamphlet No. 104. Forest Research Institute Malaysia, Kuala Lumpur, Malaysia.
- Mitchell, S.J., 1995. The windthrow triangle: A relative windthrow hazard assessment procedure for forest managers. *For. Chron.* 71, 446–450.
- Monserud, R.A., 1976. Simulation of forest tree mortality. *For. Sci.* 22, 438–444.
- Monserud, R.A., 1990. Reflections on an exercise in global modeling. In: *Forest Simulations Systems: Proc. of the IUFRO conference, Bull. 1927, Division of Agriculture and Natural Resources*. University of California, CA, pp. 383–390.
- Munro, D.D., 1974. Forest growth models: a prognosis. In: Fries, J. (Ed.), *Growth models for trees and stand simulation*, Department of Forest Yield Research. Royal College of Forestry, Stockholm, Sweden, pp. 7–21.
- Ng, F.S.P., 1978. *Tree Flora of Malaya*, vol. III. Langman Group, London, UK.
- Ng, F.S.P., 1989. *Tree Flora of Malaya*, vol. IV. Langman Group, London, UK.
- Pacala, S.W., Canham, C.D., Silander Jr., J.A., 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Can J. For. Res.* 23, 1980–1988.
- Panayotou, T., Ashton, P.S., 1992. *Not by timber alone: Economics and ecology for sustaining tropical forests*. Island Press, Washington, DC.
- Paudyal, B.K., Nik, Muhamad Majid, 1990. Preliminary thinning guideline for *Acacia Mangium* Willd. Plantations in Kemasul Forest Reserve, Peninsular Malaysia. *J. Trop. For. Sci.*, 3, 25–34.
- Pulliam, H.R., Babbitt, B., 1997. Science and the protection of endangered species. *Science* 275, 499–500.
- Ruel, J.-C., 1995. Understanding windthrow: Silvicultural implications. *For. Chron.* 71, 434–445.
- Schaetzl, R.J., Burns, S.F., Johnson, D.L., Small, T.W., 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79, 165–176.
- Sheil, D., Burslem, D.D.R.P., Alder, D., 1995. The interpretation and misinterpretation of mortality rate measures. *J. Ecol.* 83, 331–333.
- Shugart, H.H., 1984. *A theory of forest dynamics*. Spinger, NY.
- Smith, T.M., Urban, D.L., 1988. Scale and resolution of forest structural pattern. *Vegetatio* 74, 143–150.
- SPSS, 1996. *SYSTAT 6.0 for Windows*. Chicago, IL.
- Starfield, A.M., Bleloch, A.L., 1991. *Building Models for Conservation and Wildlife Management*, 2nd ed. Burgess International Group, Edina, MN.
- Swaine, M.D., Whitmore, T.C., 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75, 81–86.
- Turner, M.G., Wu, Y., Wallace, L.L., Romme, W.H., Brenkert, A., 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecol. Appl.* 4, 472–496.
- Turner, M.G., Gardner, R.H., O'Neill, R.V., 1995. Ecological dynamics at broad scales. *Science and Biodiversity Policy. BioSci. Suppl.*, pp. S29–S35.
- Urban, D.L., 1990. A versatile model to simulate forest pattern: A user guide to ZELIG version 1.0. Department of Environmental Sciences, University of Virginia, Charlottesville.
- Vanclay, J.K., 1989. A growth model for North Queensland Rainforests. *For. Ecol. Manag.* 27, 245–271.
- Vanclay, J.K., 1991. Aggregating tree species to develop diameter increment equations for tropical rainforests. *For. Ecol. Manag.* 42, 143–168.
- Vanclay, J.K., 1994. *Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests*. CAB International, UK.
- Welch, B.B., 1995. *Practical Programming in Tcl and Tk*. Prentice Hall PTR, NJ.
- Whitmore, T.C., 1972a. *Tree Flora of Malaya*, vol. I. Longman Group, London, UK.
- Whitmore, T.C., 1972b. *Tree Flora of Malaya*, vol. II. Longman Group, London, UK.
- Whitmore, T.C., 1984. *Tropical Rain Forests of the Far East*, 2nd ed. Clarendon Press, Oxford.
- Wilcove, D.S., 1989. Protecting biodiversity in multiple-use lands: Lessons from the US Forest Service. *TREE* 4, 385–388.
- Wilson, E.O. (Ed.), 1988. *Biodiversity*. National Academy Press, Washington, DC.
- Wyatt-Smith, J., Foenander, E.C., 1962. Damage to regeneration as a result of logging. *Malays. For.* 25, 40–44.