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Spatial and temporal impacts of adjacent areas on the dynamics of species diversity in a primary forest

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Introduction

During the last several decades increasingly extensive and intensive exploitation of primary tropical forests has resulted in historically unprecedented rates of deforestation. Clearcutting, conversion of forests to agricultural use or tree plantations, and construction of houses and roads have converted continuous forests into a mosaic of small remnant forest patches (Harris, 1984; Panayotou and Ashton, 1992), which are often not large enough to support local populations of many species (Powell and Powell, 1987; Malcolm, 1988; Harper, 1989; Bierragaard *et al.*, 1992; Viana and Tabanez, 1996). These forest fragments are dispersed across human-occupied landscapes and are often adjacent to managed tree plantations and non-forest areas (Schelhas and Greenberg, 1996). Significant species loss due to forest fragmentation and human activities is of major concern because species diversity is a foundation for sustainable development including production of both timber and non-timber goods (e.g., Lubchenco *et al.*, 1991; Panayotou and Ashton, 1992).

Most previous ecological research efforts have concentrated on ecological patterns and processes within a focal forest. During the past few years, however, many ecologists and government agencies have recognized the significance of studying the surrounding areas and the need for ecosystem management beyond ecological, political, and ownership boundaries (e.g., Christensen *et al.*, 1996). Ecosystem management requires a better understanding of how human disturbances such as timber logging influence ecosystem dynamics and how a focal ecosystem interacts with adjacent areas. Research on a focal ecosystem alone is usually not easy, but study of ecological impacts across boundaries is even more challenging because more variables must be considered. Interactive effects of numerous variables involved in studying landscape-scale phenomena, such as interactions between seed dispersal from outside and disturbances occurring inside a focal forest, are difficult to measure through conventional experiments or field observations. Spatially expli-

cit models could provide a useful and complementary tool (Dunning *et al.*, 1995; Turner *et al.*, 1995a).

A large number of spatially explicit forest models have been developed during the last several decades (e.g., Fries, 1974; Ek *et al.*, 1988; Urban, 1990; Pacala *et al.* 1996). Distance-dependent models consider the effects of distances among trees. This modeling approach requires that each tree be placed at a point on a spatial coordinate plane. The basic assumption is that competition among individual trees is determined by factors such as inter-tree distance and tree size (e.g., biomass, height, or diameter at breast height). The first and probably best-known distance-dependent model was built by Newnham (1964). Following Newnham's lead, numerous distance-dependent models were developed for estimating forest growth and yield (e.g., Lee, 1967; Lin, 1969; Mitchell, 1969; Bella, 1970; Hatch, 1971; Fries, 1974; Hegyi, 1974; Larocque and Marshall, 1988; Wensel, 1990).

Traditional gap models (e.g., Botkin *et al.*, 1972; Shugart, 1984) assume that light utilization differs vertically among trees. Shorter trees receive less light because taller individuals intercept light from the canopy. Conventionally, gap models consider a plot to be homogeneous and do not explicitly take account of inter-tree distance effects. Recently, however, attention has been paid to horizontal differences and interactions (Smith and Urban, 1988; Busing, 1991; Pacala *et al.*, 1993). In the ZELIG model (Smith and Urban, 1988; Urban 1990), horizontal homogeneity at the plot scale (usually 10 m) is assumed. Many individual trees are assigned to a grid cell, but the location of an individual is not specified. One of the major differences between ZELIG and its predecessors is that in ZELIG adjacent cells (or plots) interact with each other by shading and seed dispersal, while plots in conventional models operate independently. The SPACE model developed by Busing (1991) uses a much finer spatial scale (0.5 m grid cell) than ZELIG. An individual tree occupies one or more grid cells depending on tree size. Pacala *et al.* (1993) adopted the approach of distance-dependent growth-yield models (e.g., Newnham, 1964) and placed all trees on a plane according to their x - and y -coordinates.

Most spatial models ignore the characteristics and contributions of the surrounding areas to the dynamics of a focal forest (Liu and Ashton, 1995). For example, widely used gap models introduce new individuals to the modeled gap area from an external, hypothetical, constant seed pool regardless of what type of adjacent areas actually exist (Botkin *et al.*, 1972; Shugart, 1984). This assumption needs to be re-examined, however, because adjacent non-forested areas, such as industrial or agricultural land, may not provide any seeds to a focal forest. At the other methodological extreme, a recent gap model by Pacala *et al.* (1993) assumed that all the seeds were produced inside the focal area. Many forest models avoid edge effects by wrapping the modeled area onto itself (e.g., Smith and Urban, 1988) or by treating forest edges as reflecting boundaries for seeds (Clark and Ji, 1995).

Whereas hundreds of models have been built in recent years specifically for forests in temperate (e.g., Shugart, 1984; Ek *et al.*, 1988) and boreal regions (e.g., Leemans and Prentice, 1987, Bonan *et al.*, 1990), relatively few have been

developed for simulating the dynamics of tropical rainforests (e.g., Shugart and Noble, 1981; Van Daalen and Shugart, 1989; for a review see Liu and Ashton, 1995). Yet, tropical forests are the most biologically diverse on Earth and occupy 51.5% of the world's remaining forested area (Borota, 1991). The majority of the existing tropical forest models are stand models that are mainly used for predicting timber growth/yield, but which do not consider the dynamics of species richness (e.g., Vanclay, 1989).

An individual-based spatially explicit landscape model called FORMOSAIC was developed that treats the focal forest as part of the landscape mosaic, and which was applied to tropical forests (Liu and Ashton, 1998, 1999). FORMOSAIC accounts for not only the dynamics inside the focal area but also the ecological conditions of adjacent areas. This model tracks the characteristics of individual trees, including their position, size, growth, regeneration, and death. It considers both ecological and anthropogenic processes in a focal forest (e.g., recruitment, growth and death, windthrows, timber harvest), seed immigration from outside the focal forest, and other external factors such as damage done to the forest by animals like pigs. A major difference between FORMOSAIC and many other published forest models is that this model places a focal forest in a spatial location and explicitly identifies the surroundings.

In this chapter FORMOSAIC's structure, function, parameterization, validation, sensitivity and uncertainty analysis are first introduced. Then FORMOSAIC is applied to a case study from Pasoh Forest Reserve in Peninsular Malaysia involving current research on the effects of native, wild pigs on the understory plant community. Using FORMOSAIC the responses of tree species richness to interactions are evaluated among four factors: spatial scale, habitat surrounding a focal forest, harvest impact, and pig damage. In the case study, two major questions were asked: (i) how do parameters related to pig damage (e.g., percentage of area receiving pig damage, percentage of small trees killed within the damage area, and duration and timing of pig damage) change tree species richness in a focal forest? (ii) Do interactions among timber harvest, types of surroundings, and pig damage vary at different spatial scales or sizes of forest remnants? Finally, implications of the simulation results and of this modeling approach are discussed for managing forest remnants in landscape mosaics, and for understanding the mechanisms of remnant dynamics.

FORMOSAIC structure

FORMOSAIC is a spatially explicit, individual-based, stochastic model for simulating forest dynamics in landscape mosaics (Liu and Ashton, 1998). The model predicts population trajectories for individual species, species richness, stand density, and timber volume (basal area) in response to management practices, as well as biotic and abiotic factors, which influence tree recruitment, growth, and mortality.

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

grid cell, and tree location (Fig. 3.1). The landscape mosaics consist of a focal forest and surrounding areas, and the focal forest may be square or rectangular in shape. Possible surrounding areas include natural or plantation forests, clearcuts, agricultural fields, industrial land, roads, and residential buildings. In addition, the surrounding areas on the four compass sides east, west, north, and south of a focal forest may vary in structure and function. For example, Fig. 3.1 shows a case where there is an oil palm plantation on the west side of the focal forest, a species-rich forest on the east side, and non-forested areas on the north and south sides. Seeds can immigrate to the focal forest from the species-rich forest, but no seeds are available from the non-forested areas. Wild pig density is assumed to increase in response to year-round food availability in the oil palm plantation, or due to immigration from that area.

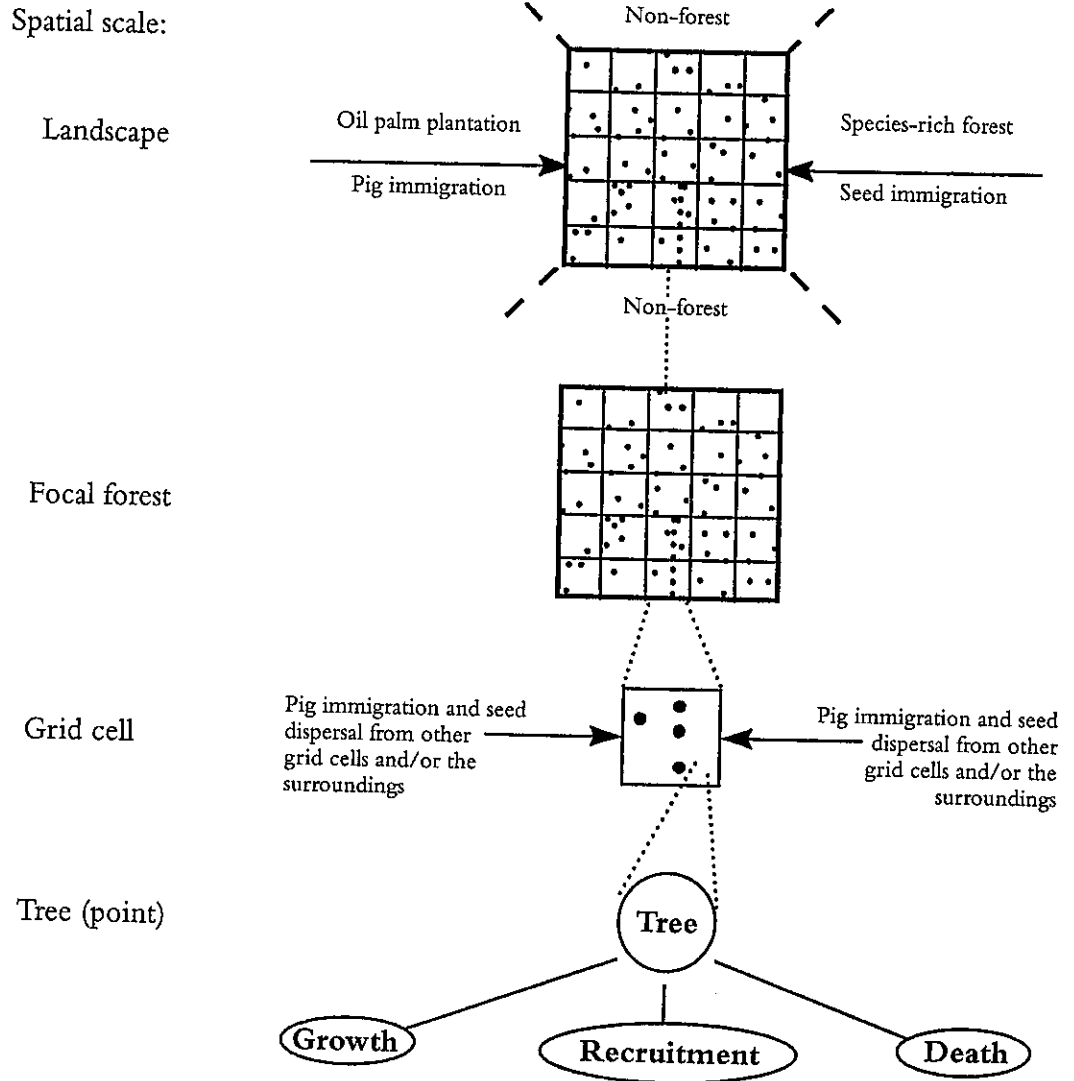
In recognition of the ecological heterogeneity within a forest, a focal forest is divided into a grid of 10 m × 10 m cells, each of which contains many individuals of different species. For example, in the 50-hectare permanent tree plot in Malaysia, there are usually 60–80 individual trees > 1.0 cm diameter at breast height (dbh), belonging to 30–50 tree species in a 10 × 10 m area (Manokaran *et al.*, 1990; Liu, unpublished data). In Fig. 3.1, the example focal forest is 0.25 ha in size and is divided into 25 grid cells. In FORMOSAIC, the size of a focal forest is only limited by computer capacity. Seeds and pigs can move 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 of each tree is explicitly mapped using *x*- and *y*-coordinates. FORMOSAIC tracks recruitment, growth, and death for each individual tree.

FORMOSAIC was programmed in the object-oriented computer programming language C++ (e.g., Ellis and Stroustrup, 1990; see Liu 1993 for an ecological application using C++). It can be implemented in UNIX (e.g., SunSparc and Silicon Graphics workstations) and PC platforms (Windows). A graphical user-interface was developed using Tcl/Tk (Welch, 1995). The exact amount of simulation time required relies on many factors like computer speed, forest size, disturbance option, management scheme, as well as output type. For example, with an Ultra II Sun workstation (167 MHz), it took about 2 minutes to finish one annual simulation (i.e., time step = 1 year) on a 50-ha forest containing more than 300 000 individual trees, and about 2 seconds to complete an annual simulation on a 1-ha forest of some 8000 trees.

FORMOSAIC parameterization

The data for parameterizing FORMOSAIC were derived mainly from the 50-ha long-term study plot in the Pasoh Forest Reserve (2°59' N, 102°18' E), Peninsular Malaysia, established in 1985 (Manokaran *et al.*, 1990; LaFrankie, 1992a, b). The Reserve is a lowland dipterocarp forest (Symington, 1943). The plot was censused in 1987 and again in 1990. All trees were mapped and tagged and their *x*- and *y*-coordinates recorded. Demographic information included diameter growth,

Fig. 3.1. Hierarchical relationship of four spatial scales (landscape, focal forest, grid cell, and tree location (point)) considered in FORMOSAIC. At the landscape scale, this schematic diagram shows that a focal forest is surrounded by three types of adjacent areas (species-rich forest, oil palm plantation, and non-forest). Seeds can immigrate into the focal forest from the adjacent species-rich forest, but no seeds are available from the neighboring non-forest. Wild pigs can immigrate into the focal forest from the oil palm plantation. Considering computational convenience and ecological heterogeneity of a forest, the focal forest (0.25 ha) is represented by a grid of 25 cells. Each cell is 10×10 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.



mortality, and recruitment. Height and crown diameter data were available from smaller subplots. Environmental data consisted of elevation, slope, and habitat. Elevation and slope were estimated on 20 × 20 m basis (i.e., all trees within a 20 × 20 m area were assumed to share the same elevation and slope). The habitat at each tree point was measured as the distance from the boundaries of swamps or streams. In the first census, over 800 tree species and more than 330 000 trees with dbh >1.0 cm were recorded in the plot.

Liu and Ashton (1998, 1999) detailed FORMOSAIC's recruitment, growth, and mortality functions and parameters, based on the empirical data from the 50-ha permanent plot. Because sample sizes in the mortality and recruitment analyses for a single species were usually small, species were grouped into four guilds: emergent, canopy, understory, and successional species. The classification was based on flora information (Whitmore, 1972*a,b*; Ng, 1978, 1989) and field knowledge of the genera including architecture, habitat, and life history (P. Ashton, personal observations; S. Thomas, personal communication). The same mortality and recruitment functions were used for all species of the same guild. In the growth analysis, rare species (<1 individual/ha) were also classified into the four guilds and a growth function for each guild was developed. All rare species in the same guild shared the same growth function. Separate growth functions were developed for each of 502 species which had relatively large population sizes (> 1 individual/ha). The growth rate of each individual tree was a function of tree size, neighborhood pressure (defined below), and specific local environmental conditions determined by elevation, slope, and distance from swamps and streams. Neighborhood pressure was measured as the total basal area of all trees in a grid cell, except the focal individual.

For mortality estimation, trees of each guild were classified into four dbh size categories: 1–5 cm, 5–10 cm, 10–30 cm, and > 30 cm. Empirical data showed that the three small size classes had significant positive relationships between mortality and tree density or basal area in a grid cell. Because the largest dbh size class (> 30 cm) did not demonstrate any relationship between mortality rate and tree density or basal area, the average mortality value was used for this class instead of a mortality function in FORMOSAIC.

Similarly, analysis from the 50-ha census data indicated that the number of new recruits in canopy, successional and understory species had negative relationships with tree density. Because the emergent species did not show any relationship with tree density or basal area, the average recruitment rate was used for this guild. FORMOSAIC assumes that recruits can be generated from seeds produced both inside a focal forest and in adjacent areas. A species in the surroundings with a higher population size is assumed to have a higher probability of providing more seeds to the focal forest (Liu and Ashton, 1998). The number of seeds input into a given grid cell is a function of seed dispersal characteristics, distance of the grid cell to the seed source area (other grid cells or adjacent area to the focal forest), availability of seeds in the seed source area, and the pre-programmed maximum number of recruits allowed in the grid cell because of competitive effects. For example, grid cells near boundaries of the focal forest will have more immigrants

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from outside of the focal forest, while more recruits near the center of the focal forest come from within the forest. The location of a seed dispersed into a grid cell is assumed to be random.

Because FORMOSAIC is individual based, it keeps information for each individual tree (e.g., species name, size, and location) until the individual dies, and use the guild information when necessary by matching the species' name with guild type. As a result, FORMOSAIC is able to examine species richness even though some information is guild-specific (Liu and Ashton, 1998).

Disturbance is very important in the dynamics of species richness (Connell, 1979). Thus, FORMOSAIC considers three major forms of disturbance: timber harvest, windthrow, and pig damage. The rationale to include them in FORMOSAIC and the modeling methods are discussed below.

Timber harvest

The cutting of wood for commercial use is pervasive in Southeast Asia, and few reserves are free from this pressure. Any model which cannot incorporate the effects of logging will have minimal applicability to real-world forest reserves. In Tropical Asian forests timber trees are classified as dipterocarps or non-dipterocarps, due to the unusual dominance of the family Dipterocarpaceae in species diversity and basal area in the canopy and emergent tree size classes. Non-dipterocarp timber species are those which can reach timber size but are in other families (Wyatt-Smith, 1952). The Dipterocarpaceae has about 10 genera and 170 species in Peninsular Malaysia and historically has contained the most important commercial timber species in Malaysia (Appanah and Weinland, 1990). As the demand for timber products has grown, however, the value of non-dipterocarp wood has increased and greater numbers of non-dipterocarp species are being harvested to meet this demand (Manokaran and Swaine, 1994). According to Appanah and Weinland (1993), 30 dipterocarp and 90 non-dipterocarp timber species were recorded in the 50-ha plot at Pasoh forest reserve. FORMOSAIC can change the minimum size for harvest, length of rotation cycle, species harvested, and harvest location so that consequences of various harvest strategies can be assessed.

Timber logging can have significant impacts on residual trees because of tree fall, road construction, and machinery movement (Whitmore, 1984; Schatzel *et al.*, 1989). For the sake of simplicity, it was assumed that a tree may fall randomly along one of the four compass directions: north, south, east, or west. It was further assumed that the size of the impact zone (*IZ*) was positively related to the size of a fallen tree:

$$IZ = LZ \times WZ$$

where *L* and *W* are two parameters (> 0) which determine the size of an impact zone. *LZ* is the length of the impact zone:

$$LZ = L \times H$$

where H is the height of a fallen tree, and WZ is the width of the impact zone:

$$WZ = W \times C$$

where C is the crown radius of a fallen individual.

Within the impact zone, a proportion (P) of the trees smaller than a fallen tree would be destroyed. FORMOSAIC allows the user to change the value of P , L and/or W to simulate different degrees of logging impact on species richness in a focal forest. The impacts due to road construction and machinery movement were not separated from tree falling. Rather, to simplify computation, these impacts were incorporated into the calculation of the impact zone and proportion of smaller trees destroyed.

Windthrow

Windthrow is an important force in shaping forest dynamics (Crow, 1982; Pacala *et al.*, 1993), with the amount of tree damage changing in relation to windthrow frequency, intensity, and location as well as stand conditions such as tree height (Ruel, 1995; Mitchell, 1995). Although windthrows are thought to be fairly common at Pasoh (H. T. Chan, personal communication), there is little information available in regard to the frequency and intensity of windthrow damage in the study site. It was assumed that a windthrow would affect a certain area in which large trees would be blown over, and the falling of these large trees would in turn damage some proportion of smaller trees within the impact zone. The impact zone is calculated as the area determined by the height times the crown radius of a fallen tree. To allow for simulations of various windthrow impact scenarios, in FORMOSAIC it is feasible to change the value of windthrow frequency, location of windthrow impact within a focal forest, minimum dbh size of fallen large trees, proportion of large trees in the impacted area falling due to windthrow, and proportion of smaller trees killed by fallen large trees within the impact zone.

Oil palm

Oil palm was first planted in Malaysia in 1917 (Williams and Hsu, 1970), and the rate of planting greatly accelerated in the 1960s and 1970s. By 1980 there were a million hectares of oil palm plantations (Hartley, 1988) and the rate is steadily increasing as more and more rubber tree plantations are converted to oil palm. The trees fruit continuously. When harvested by workers using long poles, the fruit assemblage crashes to the ground and numerous small palm kernels roughly 1.5 cm in diameter are scattered by the impact. Not all fruits on the ground are taken by workers. Local hunters believe that pigs can survive and even thrive on a diet comprised almost entirely of the fallen, uncollected palm fruits. Various studies have showed that pig density is limited by food (Giffin, 1978; Singer, 1981;

Baber and Coblenz, 1986; Caley, 1993), and in Malaysia pig density was historically also probably regulated by food availability. The mast-fruiting phenomenon of many tree species in southeast Asia may have limited pig densities in Malaysia because of the lack of food availability in non-mast fruiting years. Now, however, the palm fruits of oil palm plantations have created an almost limitless food supply, and this is the probable cause of the unusually high pig density recently seen in Malaysia. Only hunting pressure outside of the reserves may be regulating the pig population densities. Oil palm was chosen as a surrounding matrix for focal forests in FORMOSAIC because it is already so prevalent in Peninsular Malaysia and quickly becoming more so in Sabah, Sarawak, and Indonesia, in addition to some South American countries. Also, Pasoh Forest Reserve has been virtually surrounded by mature oil palm plantations for almost 20 years.

Pig damage

An increasing number of studies have documented the powerful effects that large populations of mammalian herbivores can have on the plant community. Examples include white-tailed deer (Whitney, 1984; Frelich and Lorimer, 1985), elephants (Buechner and Dawkins, 1961; Barnes *et al.*, 1994), beavers (Johnston and Naiman, 1990), and pikas (Huntly, 1987). In the Pasoh Forest Reserve, the damage to understory trees caused by wild pigs is extremely high, and has recently become the focus of several research projects (K. Ickes, unpublished data).

The wild pig (*Sus scrofa*) has a broad natural distribution, ranging from Northern Africa throughout Europe and Asia as far southeast as Peninsular Malaysia. As an invasive species they often reach high population densities and are being increasingly cited as a major threat to local species or ecosystems in many parts of the world (Bratton, 1974, 1975; Lacki and Lancia, 1986; Coblenz and Baber, 1987; Crome and Moore, 1990; Vtorov, 1993). Pigs are truly omnivorous and will eat acorns, worms, roots, tubers, seeds, fruits, leaves, twigs, grass, agricultural crops, and many other types of food (Giffin, 1978).

The reproductive biology of pigs is conducive to rapid population growth, which has also presumably contributed to their success as an invasive or pest species. In contrast to other ungulates, pigs have very high reproductive potential; puberty is reached at a very early age (as early as 7 months), females are polyestrous, litters are large (up to ten), and gestation and lactation periods are short, permitting up to two litters per year (Giffin, 1978; Singer, 1981; Graves, 1984). In most temperate habitats the breeding of wild pigs tends to be rather seasonal, but in wetter temperate habitats such as riparian forest and tropical areas they have been observed to breed twice a year or year-round (Giffin, 1978; Sweeney *et al.*, 1978; Singer, 1981; Baber and Coblenz, 1986; Coblenz and Baber, 1987; Saunders, 1993; K. Ickes, personal observations).

Although there are no older estimates of pig densities in Peninsular Malaysia, communications with long-term field biologists and people living in rural settings regularly indicate that pig densities have increased dramatically over the past several

decades (H. T. Chan, personal communication). Pig densities in Europe and Asia, including tropical southern Asia, are usually around 2.5 individuals/km² (Singer, 1981; Karanth and Sunquist, 1992, 1995). Preliminary results from the Pasoh Forest Reserve document densities of 20–80 pigs/km² (K. Ickes, unpublished data). This unusually high density may be due to three possible causes: (i) the population of tigers (the major predator of the pigs) has been declining since the 1960s; (ii) no hunting is permitted within Pasoh Forest Reserve; and (iii) the reserve is virtually surrounded by oil palm tree plantations, the fallen fruits of which provide a practically limitless food supply. Pigs can often be seen feeding in the palm plantation along the edge of the forest.

Pigs have various behavioral characteristics which affect the plant community in Malaysia, but only one has been used specifically in FORMOSAIC: nest building. At “normal” pig population levels this behavior probably does not contribute significantly to plant community dynamics. At pig densities of 10 to 40 times the historic levels, however, the impacts are quite pronounced, with possible long-term effects on plant species diversity and distribution.

In Malaysia, when close to delivering her litter, a female pig constructs a fairly large dome-shaped nest. Pigs seem to use a wide variety of vegetative matter for this construction, utilizing whatever materials are nearby; at Pasoh, they use almost entirely saplings (K. Ickes, unpublished data). To construct a nest, the female pig approaches a sapling, turns her head to the side to grasp it in her jaws, and then jerks her head powerfully upright. If the ground is water-logged, the entire sapling is usually uprooted, but if the soil is held tighter to the roots then the trunk is snapped off (K. Ickes, personal observation). In either case, the bole with all the foliage is dragged to the nest site and carefully added to the growing mound. When complete, the female crawls underneath and births her young (Medway, 1963; K. Ickes, personal observation).

Nest size is extremely variable (K. Ickes, unpublished data) and is presumably determined by the size of the pig. Not only does the number of trees used to construct each nest vary, but so does the size of the trees taken. Some nests have only 150 saplings (all less than 2 m in height), whereas others have over 500 saplings (some more than 4 m in height). Similarly, the area affected by a pig removing trees is quite variable. Based on a sample of ten nests in the 50-ha plot, an average of 310 trees were taken per nest from an area of roughly 180 m² (K. Ickes, unpublished data). This represented over 50% of the number of stems over 70 cm tall and less than 2.5 cm DBH in that same 180 m² area. Even if it is assumed that areas damaged by pigs when making nests do not overlap, then roughly 20% of the 50-ha plot would have lost 50% of its total understory cover. The number of pig nests is quite high in the 50-ha permanent plot. For example, over a one-year period 152 new nests were constructed in 25 hectares (K. Ickes, unpublished data).

In FORMOSAIC, it is possible to adjust the maximum size of trees which are damaged by the pigs, location of damage, duration and timing of damage, and proportion of trees damaged in the impacted area of a focal forest. The ability to

change these parameters allows for the estimation of the impacts of pigs on the plant community at different pig densities and damage scenarios.

Validation, sensitivity and uncertainty analysis

Validation

Half of the census data (1987 and 1991) from the 50-ha plot was used for FORMOSAIC development. The other half of the data was reserved for model validation. Using the 1987 data as initial input and running the model for the same length of time period as the time difference between the two censuses, the simulation results from FORMOSAIC fit the 1991 census data well in terms of species richness, number of trees, and basal area at two spatial scales (0.25 ha and 2.5 ha) (Liu and Ashton, 1998). At the scale of 0.25 ha, *p* values (from paired *t*-tests) for mean species richness, stand density and basal area from simulations and observations were 0.85, 0.84, and 0.97, respectively. At the scale of 2.5 ha, the *p* values for the three indices were 0.16, 0.19, and 0.27, respectively.

Sensitivity analysis and uncertainty analysis

A sensitivity analysis is used to test how model output responds to small changes in parameters of interest (Jorgensen, 1986; Turner *et al.*, 1994; Starfield and Bleloch, 1991). Uncertainty analysis is employed to identify how model results vary with large variances in parameters when the values of parameters have too much uncertainty. Both types of analysis are useful in modeling and simulation studies. Sensitivity analysis can be used to detect parameters that strongly influence the simulation results. In cases where empirical estimates of model parameters are uncertain or management parameters have a wide range, uncertainty analysis is helpful in detecting the degrees of impacts within a reasonable range of parameters (e.g., within two extremes). In addition, uncertainty analysis can detect non-linear relationships between an independent variable and a dependent variable over a wide range of values.

Sensitivity and uncertainty analyses were conducted on nine parameters related to windthrow, timber harvest impact, and immigration from the surroundings at the scale of 0.25 ha (Liu and Ashton, 1998). Sensitivity analysis and uncertainty analysis indicated that the minimum size of timber trees for harvest was the most sensitive parameter for species richness, basal area, and number of trees in a focal forest. Species richness was also very sensitive to duration of immigration from surrounding forests and minimum tree size felled by windthrows. The second and third most sensitive parameters for number of trees were proportion of smaller trees killed in the harvest impact zone and duration of immigration. For basal area, the two other most sensitive parameters were proportion of smaller trees killed in the harvest impact zone and minimum tree size felled by windthrows (Liu and Ashton, 1998). Uncertainty analysis indicated that in most cases the relationships

between species richness (or basal area, or number of trees) and each of the nine parameters were non-linear.

Case study: species richness affected by type of surroundings, timber harvest, and pig damage

Simulation methods

In order to address our study questions, 39 different simulations were designed to be run by FORMOSAIC (Table 3.1). Any two simulations might differ in one or more factors including spatial scale of a focal forest, type of surroundings, harvest impact, and degree of pig damage.

Spatial scales

Because forest remnants differ in size, simulations were run at five spatial scales: 0.25 ha (50 m × 50 m), 1 ha (100 m × 100 m), 4 ha (200 m × 200 m), 9 ha (300 m × 300 m), and 25 ha (500 m × 500 m). To avoid shape effects, all simulated forests were squares. To best achieve a balance between computational time and the size of many forest remnants, most simulations were done at the scale of 4 ha.

Type of surroundings

To evaluate the impacts of different types of surrounding areas on species richness within a focal forest, we created two types of surroundings: species-rich forest and oil palm plantations on all four sides of a focal forest. A species-rich forest in this study refers to a forest with the same species richness and composition as the 50-ha permanent plot, which has more than 800 tree species (LaFrankie, 1992a). Although there are many species grown monoculturally in tree plantations in tropical countries, such as rubber trees, fruit trees and commercial timber trees (Lamprecht, 1989), in our simulations only single-species plantations of the oil palm were used, a very important economic species occupying vast amounts of land in Malaysia (e.g., Williams and Hsu, 1970; Hartley, 1988). Furthermore, it was assumed that a focal forest could receive seeds from the adjacent species-rich forests but that no seeds entered the focal forest from oil palm plantations.

Harvest impact

Dipterocarps and non-dipterocarps are usually harvested at a minimum size of 50 and 45 cm, respectively (Appanah and Weinland, 1990). Our simulations followed this criterion in determining timber trees eligible for harvest. The first harvest would take place at year 10, with a rotation length of 30 years after that. Our harvest strategy can be classified as selective cutting, as only timber trees of at least 45 cm were harvested. Under harvest, the size of the impact zone was $(2 \times H) \times (2 \times C) = 4 \times H \times C$ (both L and W were assumed to be 2, see the section on FORMOSAIC Parameterization). It was further assumed that 80% (P) of the smaller trees within the impact zone were killed. This heavy impact regime may

Table 3.1. *Simulation scenarios*

Scale (ha)	Type of surroundings	Harvest impact	Percentage of small trees damaged by wild pigs	Percentage of area receiving pig damage	Duration of pig damage (years)	Timing of pig damage (years)
0.25	Oil palm plantation	yes	60	100	100	1-100
0.25	Oil palm plantation	no	60	100	100	1-100
0.25	Species-rich forest	yes	0	0	0	1-100
0.25	Species-rich forest	no	0	0	0	0
1	Oil palm plantation	yes	60	100	100	1-100
1	Oil palm plantation	no	60	100	100	1-100
1	Species-rich forest	yes	0	0	0	0
1	Species-rich forest	no	0	0	0	0
4	Oil palm plantation	no	20	100	100	1-100
4	Oil palm plantation	no	20	100	50	1-50
4	Oil palm plantation	no	20	100	50	51-100
4	Oil palm plantation	no	20	25	100	1-100
4	Oil palm plantation	no	20	25	50	1-50
4	Oil palm plantation	no	20	25	50	51-100
4	Oil palm plantation	no	60	100	100	1-100
4	Oil palm plantation	no	60	100	50	1-50
4	Oil palm plantation	no	60	100	50	51-100
4	Oil palm plantation	no	60	25	100	1-100
4	Oil palm plantation	no	60	25	50	1-50
4	Oil palm plantation	no	60	25	50	51-100
4	Oil palm plantation	no	60	100	75	26-100
4	Oil palm plantation	no	60	100	25	76-100
4	Oil palm plantation	no	60	100	75	1-75
4	Oil palm plantation	no	60	100	25	1-25
4	Oil palm plantation	no	40	100	100	1-100
4	Oil palm plantation	no	100	100	100	1-100
4	Oil palm plantation	no	60	75	100	1-100
4	Oil palm plantation	no	60	50	100	1-100
4	Oil palm plantation	no	0	0	0	0
4	Oil palm plantation	yes	60	100	100	1-100
4	Oil palm plantation	no	60	100	100	1-100
4	Species-rich forest	yes	0	0	0	0
4	Species-rich forest	no	0	0	0	0
4	Oil palm plantation	yes	60	100	100	1-100
9	Oil palm plantation	no	60	100	100	1-100
9	Species-rich forest	yes	0	0	0	1-100
9	Species-rich forest	no	0	0	0	0
25	Oil palm plantation	yes	60	100	100	1-100
25	Oil palm plantation	no	60	100	100	1-100
25	Species-rich forest	yes	0	0	0	0
25	Species-rich forest	no	0	0	0	0

occur when powerful machinery such as crawler tractors are used (Panayotou and Ashton, 1992). The surrounding forests were intact. Only timber trees in a focal forest were eligible for harvest.

Pig damage

Four parameters were considered related to pig damage: percentage of trees < 3cm dbh damaged, percentage of area receiving pig damage, duration of pig damage, and timing of pig damage. In the simulations different percentages of small trees damaged by the wild pigs were set (0%, 20%, 40%, 60%, and 100% of the small trees within the pig damage area). Percentage of area receiving pig damage ranged from 0%, 25%, 50%, 75%, to 100% of the entire focal forest.

Duration of pig damage refers to the number of years that the wild pigs have been building nests in the focal forest. In our simulations, duration of pig damage was 0, 25, 50, 75 or 100 years. Twenty-five years was chosen as a duration interval because oil palm plantations' life cycle is about 25 years (Williams and Hsu, 1970). It was assumed that without abundant fruits from the surrounding palm plantations, pig densities would be low and therefore damage to small trees in nearby primary forests would be not significant. Damage duration of 0 years may be equivalent to a situation in which there are no oil palm plantations in the surroundings, and hence pig densities have not been artificially elevated.

Timing of pig damage defines when, or during which years, damage takes place. For example, pig damage could occur in different periods of time corresponding to the existence of oil palm plantations. If two 25-year rotations are thought to be the maximum yield possible for growing oil palm, after which time the surrounding land is left to regenerate to forest, pig damage with a duration of 50 years could be input for the first half of a 100-year simulation, with no damage occurring in the last 50 years.

Data for simulation initialization

To initialize a simulation, we used the environmental data of slope, elevation, and location of streams and swamps from the 50-ha plot at Pasoh. In addition, tree data including dbh, location, and species were obtained from the 1987 census. The 50-ha plot is rectangular, running 0–1000 m west to east, and 0–500 m south to north. Therefore, a simulated focal area of 50 m × 50 m would employ the known topographic relief and the 1987 tree survey information for the 0.25-ha area lying 0–50 m west to east and 0–50 m south to north within the 50-ha plot. Similarly, a simulated focal area of 500 m × 500 m would use information from the 25-ha area of 0–500 m west to east, and 0–500 m south to north within the 50-ha plot. A simulated focal area was assumed to be embedded in one of the two types of surroundings described previously.

Liu and Ashton (1998) reported that simulations of high frequency and intensity of windthrows for this forest usually lower species richness. In this study, it was assumed that windthrows had the same frequency and severity, starting at year 20 and occurring subsequently once every 40 years. When a windthrow took place,

20% of the trees with > 30 cm in dbh were assumed to be blown down and 20% of the smaller trees within the impact area (height \times crown radius of a fallen tree) were presumably destroyed. Windthrows were included in all the simulations because they are thought to be an important force in shaping forest dynamics (Crow, 1982; Pacala *et al.*, 1993) and have recently occurred in the Pasoh Forest Reserve (H. T. Chan, personal communication). Because the purpose of this paper is not to assess the impacts of windthrows but rather to evaluate the interactive effects of surroundings, timber harvest, and pig damage on species richness, the same windthrow frequency and severity were maintained for all simulations.

Calculation of average species richness and statistical tests

Each simulation step was 1 year and each run lasted 100 years. Those simulations at the scale of 9 ha or larger had five replicates. Smaller scales had ten replicates. Simulations at small spatial scales were replicated to a greater extent because FORMOSAIC is a stochastic model and small scales tended to have higher variations among replicates. The average species richness was calculated over the entire simulation period of 100 years and across replicates. To detect main effects of variables and their interactions on species richness and to test for significance of differences in average species richness among various simulation scenarios, ANOVA and Bonferroni tests were used for multiple comparisons in SYSTAT (SPSS Inc., 1996).

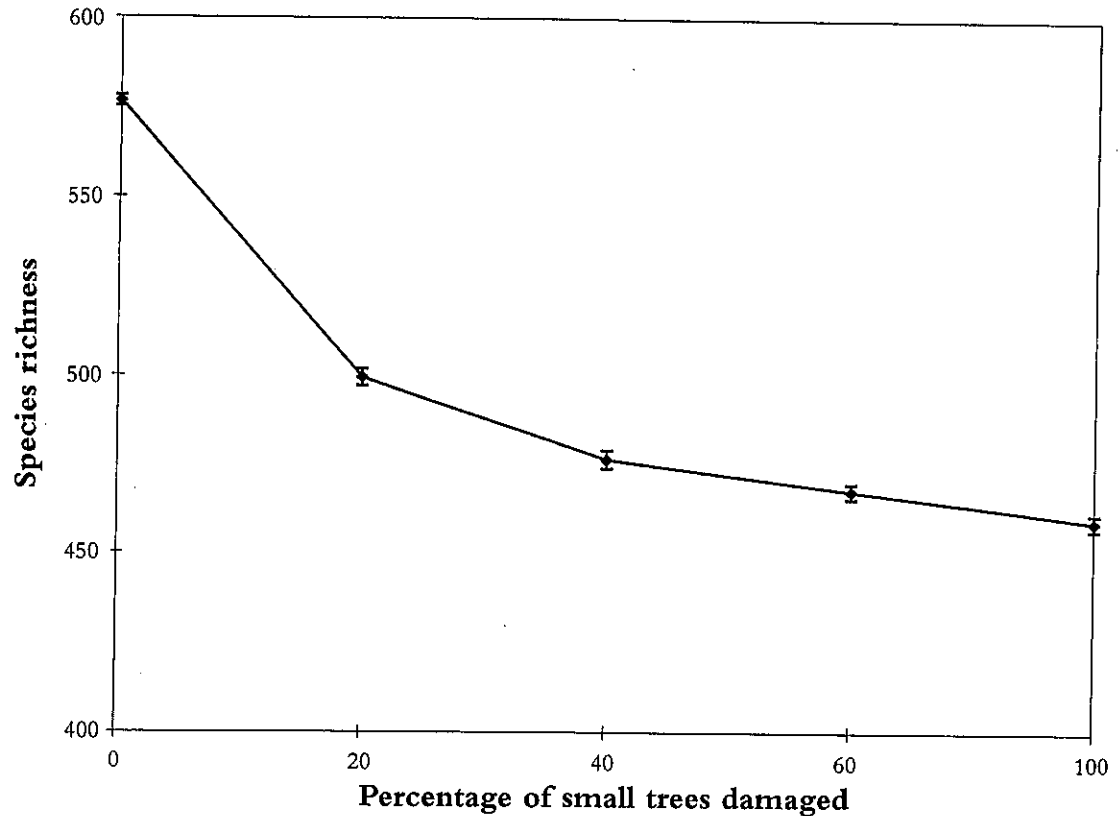
Simulation results

Average species richness decreased with increases in percentage of small trees damaged by wild pigs (Fig. 3.2). Species richness dropped rapidly between 0 and 20%, but as the percentage of small trees damaged increased from 20% to 100% the rate of decline in species richness was much lower. Species richness had a negative linear relationship with percentage of pig damage area (Fig. 3.3). With regard to the impact resulting from duration of pig damage, species richness was sharply reduced during the first 25 years, but showed little change in the latter 75 years (Fig. 3.4). There were very strong interactions among percentage of small trees damaged, percentage of area receiving pig damage, and duration of pig damage (Table 3.2).

Timing of pig damage was also important for species richness. Damage during the early years of simulations resulted in much lower average species richness after 100 years than damage during the late years of simulations (Fig. 3.5). It was clear that species richness was sharply lowered due to the first few years of pig damage (Fig. 3.6), while subsequent damage in later years did not influence species richness as much.

Species richness was scale-dependent and varied significantly due to the interactions among types of surroundings, timber harvest impact, and pig damage (Fig. 3.7). When a focal forest was surrounded by species-rich forests with no harvest impact and no pig damage, species richness was always the highest, regardless of how large a focal forest was. The combination of being surrounded by plantations

Fig. 3.2. Effects of percentage of small trees damaged by wild pigs on species richness in a 4-ha forest. In the simulations, timber trees were not harvested. Pig damage took place continuously in the entire forest. The focal forest was surrounded by oil palm plantations. Results are means ($n = 10$) for 100-yr simulations. Error bars indicate two standard errors.

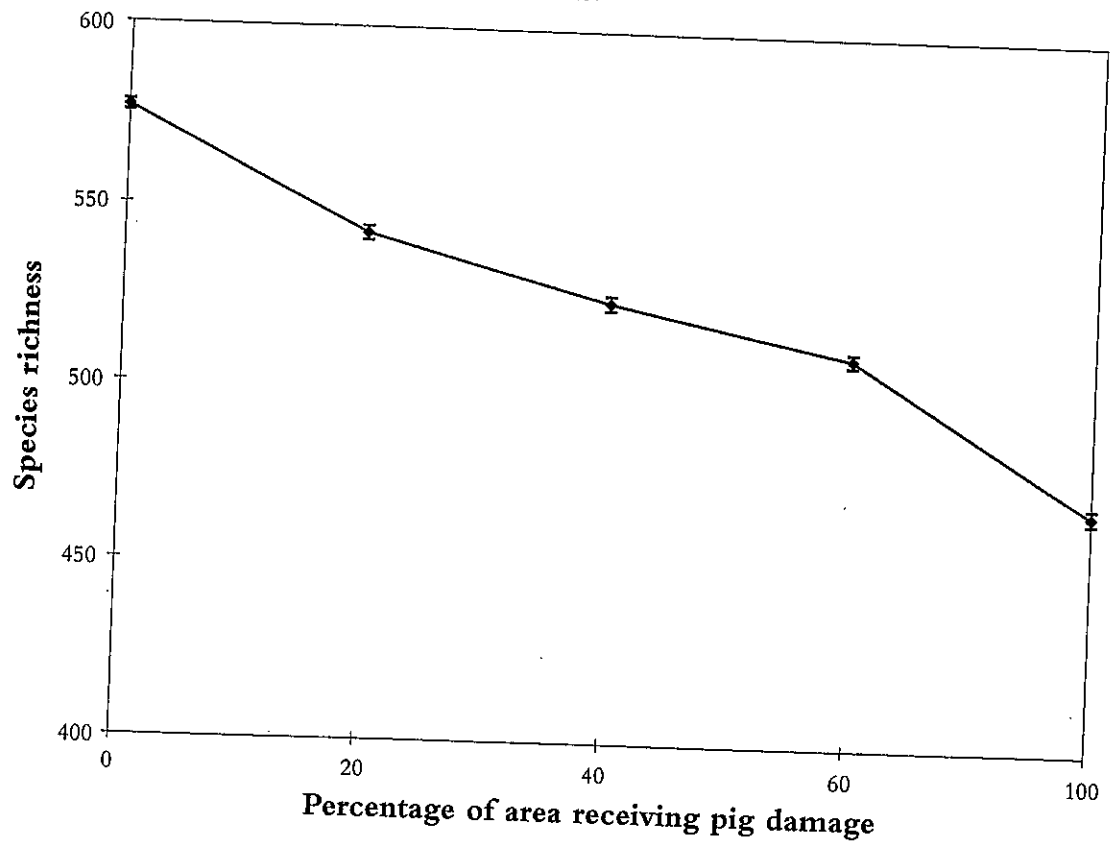


with harvest impact and pig damage led to the lowest species richness across spatial scales. Species-rich surroundings with harvest and no pig damage resulted in higher species richness than oil palm plantations with pig damage and no harvest at scales of less than 4 ha, but lower species richness at scales of 4 ha or larger.

Discussion

FORMOSAIC mimics forest dynamics in fragmented and heterogeneous landscape mosaics, which represent a common pattern of forest distribution (Shugart, 1984; Harris, 1984; Schelhas and Greenberg, 1996). Ecological processes and patterns may vary at different spatial scales (e.g., Levin, 1992; Turner *et al.*, 1995b). FORMOSAIC is able to run simulations at multiple spatial scales and provides a tool to incorporate the effects of timber harvest and ecological processes inside a focal forest with those of seed and pig immigration from the surroundings of the

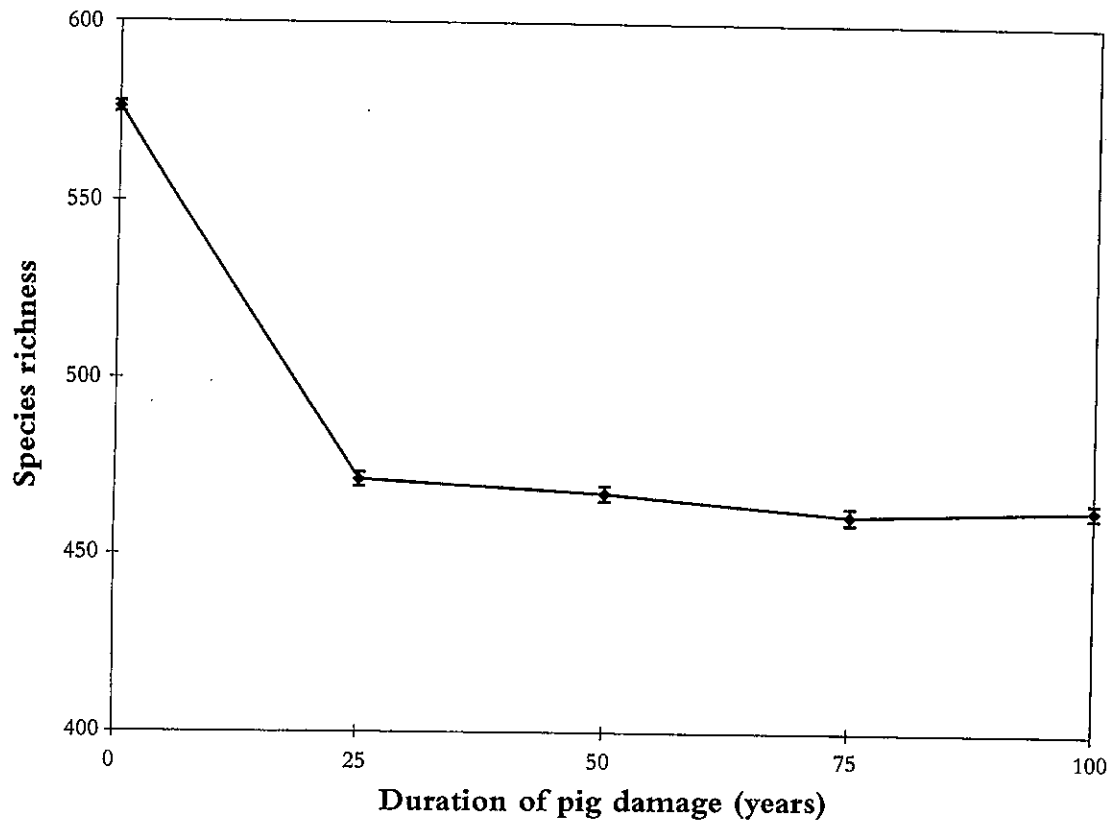
Fig. 3.3. Effects of percentage of area with pig damage on species richness in a 4-ha forest. In the simulations, timber trees were not harvested. Pig damage took place continuously, with 60% of small trees (<3 cm in dbh) damaged. The focal forest was surrounded by oil palm plantations. Results are means ($n = 10$) for 100-yr simulations. Error bars indicate two standard errors.



focal forest. Our simulations indicated that type of surroundings, harvest impact, and pig damage had major impacts on maintenance of species richness in a focal forest, and that their roles varied among spatial scales (Fig. 3.7).

FORMOSAIC is quite different from a typical gap model (Botkin *et al.*, 1972; Shugart, 1984). First, it explicitly considers the impacts (e.g., seed and wildlife immigration) from the surroundings, whereas a typical gap model does not. Second, it simulates the dynamics of an entire forest (which may consist of both gaps and non-gaps at the same time), while 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, while 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

Fig. 3.4. Impacts of duration of pig damage on species richness in a 4-ha forest. In the simulations, timber trees were not harvested. Sixty percent (60%) of small trees (< 3 cm in dbh) were damaged in the entire forest. The focal forest was surrounded by oil palm plantations. Results are means ($n = 10$) for 100-yr simulations. Error bars indicate two standard errors.



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

Individual-based spatially explicit models like FORMOSAIC need large amounts of individual-based and spatial data collected in the field. The process of collecting fine-scale data in the field (in our case, the Pasoh forest) is quite time-consuming. However, this modeling approach is useful for in-depth study of long-term species diversity dynamics. Hopefully, the challenge of data collection can be met by future remote sensing techniques, although current remote sensing technologies are not able to classify tree species (especially understory species) as accurately as plant systematists, and the spatial resolutions regarding locations of individual trees in remote sensing imagery are not as accurate as field measurements.

Table 3.2. Analysis of variance for the main and interactive effects (in a 2^3 factorial design) of percentage of small trees damaged by wild pigs (PSTD, 20% and 60%), percentage of area with pig damage (PAPD, 25% and 100%), and duration of pig damage (DPD, 50 and 100 years) on species richness in a 4-ha forest.

Source	Sum-of-squares	DF	Mean-square	F-ratio	P
PSTD	1402.98	1	1402.98	313.88	< 0.001
DPD	27008.31	1	27008.31	6042.393	< 0.001
PAPD	21108.428	1	21108.428	4722.451	< 0.001
PSTD×DPD	1469.755	1	1469.755	328.819	< 0.001
PSTD×PAPD	1274.805	1	1274.805	285.204	< 0.001
DPD×PAPD	15242.653	1	15242.653	3410.139	< 0.001
PSTD×DPD×PAPD	966.398	1	966.398	216.206	< 0.001
Error	321.826	72	4.47		

When the duration of pig damage was 50 years, pig damage occurred from years 51–100. In the simulations, timber trees were not harvested. The 4-ha focal forest was surrounded by oil palm plantations.

Fig. 3.5. Relationship between timing of pig damage and species richness in a 4-ha forest. In the simulations, timber trees were not harvested. When pig damage took place, 60% of small trees (< 3 cm in dbh) were damaged in the entire forest. The focal forest was surrounded by oil palm plantations. Results are means ($n = 10$) for 100-yr simulations. Error bars indicate two standard errors.

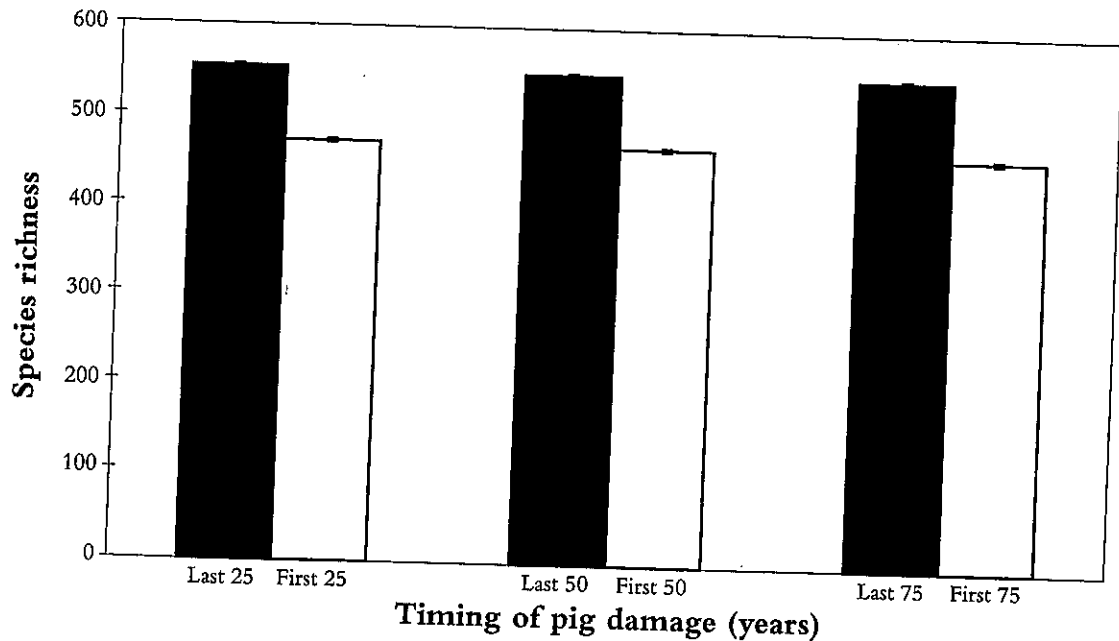
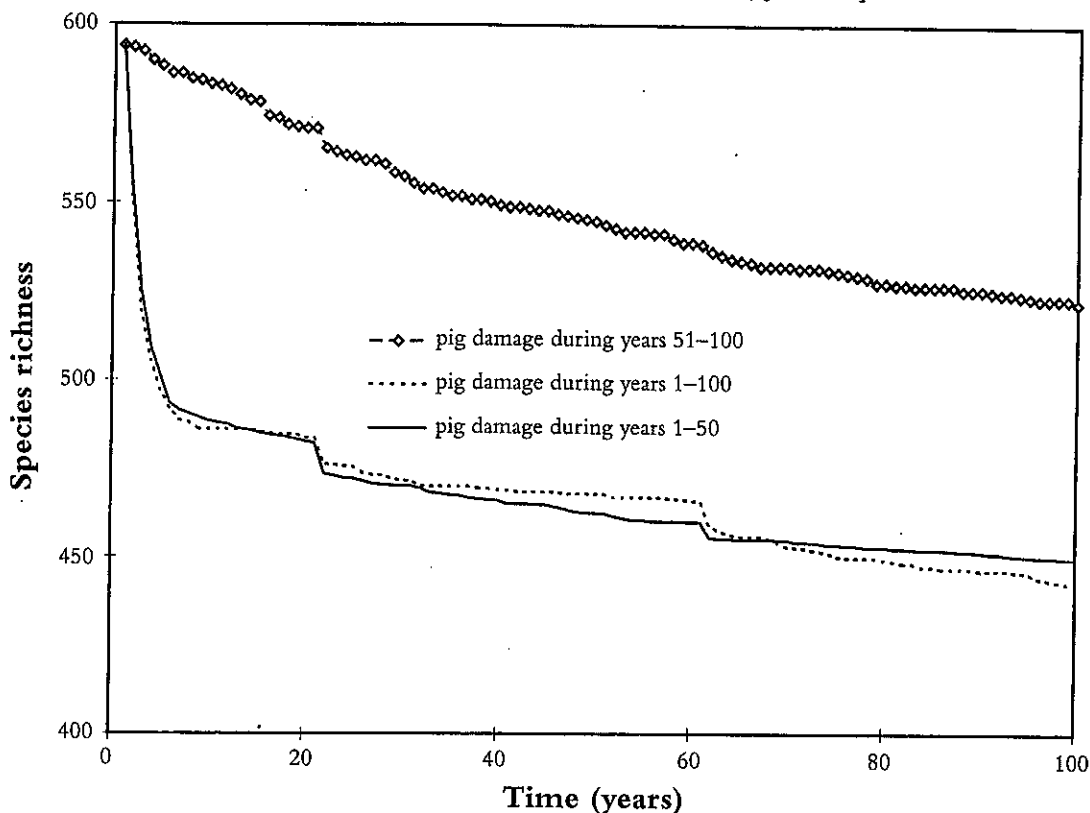


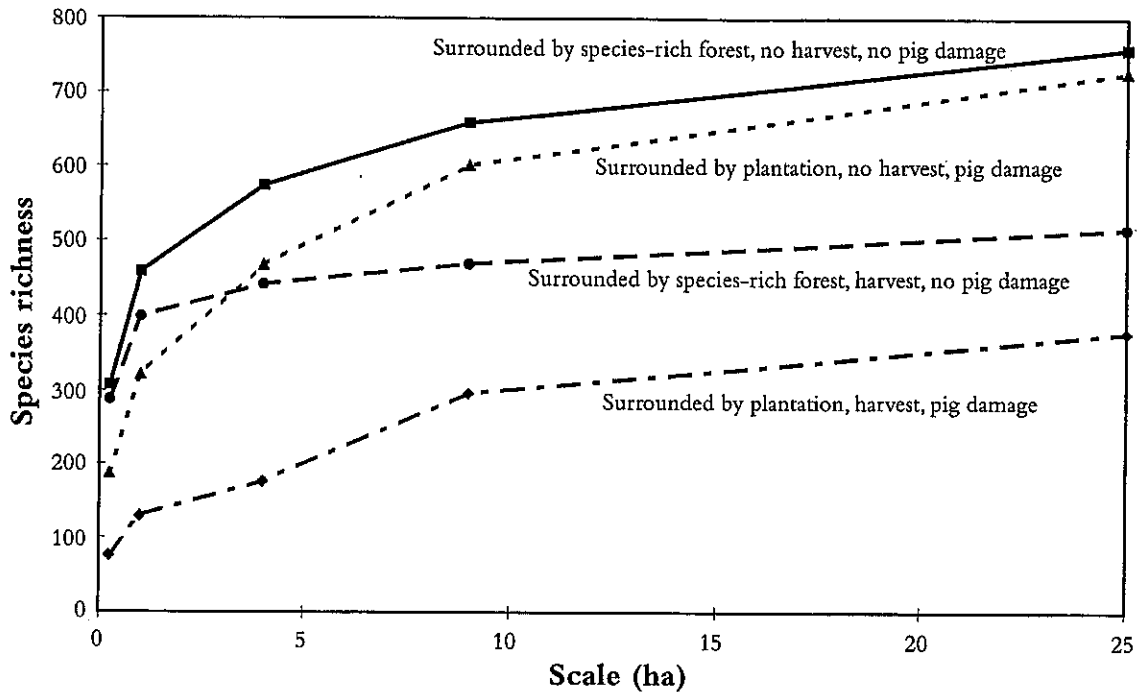
Fig. 3.6. Dynamics of species richness in a 4-ha forest with different timing of pig damage. In the simulations, timber trees were not harvested. When pig damage took place, 60% of small trees (< 3 cm in dbh) were damaged in the entire forest. The focal forest was surrounded by oil palm plantations. Results are means ($n = 10$) for 100-yr simulations.



Results obtained regarding impact of wild pigs on tree species diversity are not consistent with the widely supported “intermediate disturbance hypothesis,” which states that species diversity peaks under intermediate disturbance (Connell, 1979). Simulation results in our case study, however, indicate a monotonic decrease of species diversity with increase in the degree of pig damage. We believe that the reason is that the wild pigs destroy only small trees. Damage to small trees creates small gaps, which do not provide sufficient niches for new species to colonize. However, in many simulations where large trees were harvested or large gaps were generated, FORMOSAIC did produce outputs supporting the “intermediate disturbance hypothesis.” For example, an intermediate rotation length resulted in the highest species diversity (Liu and Ashton, 1998).

As is well known, realistic models have to depend on realistic data. However, it is not always easy to obtain adequate data for parameterizing and validating the models. In addition to logistic issues such as money and personnel, serious attention

Fig. 3.7. Interactive effects of type of surroundings, harvest impact, and pig damage on average species richness along spatial scales. When pig damage took place, 60% of small trees (< 3 cm in dbh) were damaged in the entire forest. Results are means ($n = 10$ for spatial scales of < 9 ha and $n = 5$ for spatial scales of ≥ 9 ha) for 100-yr simulations.



should be paid to the methodology of data collection because studying ecological processes and patterns beyond boundaries are more complicated than studying a focal forest alone. In this study timing and duration of pig damage were used as surrogates to represent dynamic change of the surroundings. Such measures do not simulate the spatial dynamics of the whole complex of landscape mosaics. Better understanding and simulation of forest and wildlife dynamics in the adjacent areas could enhance model predictability. In the Pasoh Forest Reserve, field study on pig damage to small trees in the 50-ha permanent plot is under way (K. Ickes, unpublished data). Much more information on the relationships between pig damage (e.g., percentage of small trees damaged, area receiving pig damage, and duration and timing of pig damage) and pig population dynamics due to adjacent oil palm plantations is still needed.

Visitors to the Pasoh Forest Reserve are often shocked by the damage caused by the making of even one pig nest. Pigs are removing a substantial percentage of the understory in some areas (K. Ickes, personal observations), and this must have some impact on both plant and animal community ecology. For example, understory tree species often fruit year-round, with low numbers of fruit at any given time, and various bird species rely on the fruits of these trees for food.

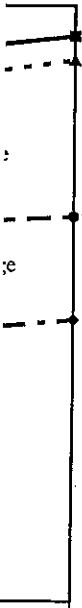
Obviously, the quantity of available fruits for these birds is much lower in areas with multiple pig nests. Similarly, less foliage will mean fewer arthropods for insect eating birds and vertebrates. If pigs are preferentially selecting certain tree species for nests and avoiding others, then the relative abundance or distribution of those tree species could be substantially altered. The impacts of a dense pig population on the primary forests are thus potentially numerous and critical.

Our simulation results may have important implications for guiding future field study, for conserving tree species richness in primary forests, and for managing oil palm plantations. For example, because a low percentage of small trees damaged by wild pigs could reduce species richness dramatically (Fig. 3.2), it is necessary to accurately measure the damage caused by wild pigs. Oil palm plantations should not be near primary forests, or the oil palm fruits on the ground should be immediately collected so that they will not provide food for wild pigs, thus hopefully reducing pig population size.

In this case study an attempt was made to explicitly address the interactions among adjacent areas, timber harvest, and pig damage, as well as their impacts on species richness of a tropical forest. This approach could be also useful for understanding the dynamics of tree species richness in temperate and boreal forest zones, because there are many similarities (e.g., fragmentation, Harris, 1984) among various forest types. Simulations that study ecological processes and patterns within and across ownership and management boundaries have the potential to provide valuable information for resource management from a landscape perspective (Liu and Ashton, 1999).

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