SIMULATING EFFECTS OF LANDSCAPE CONTEXT AND TIMBER HARVEST ON TREE SPECIES DIVERSITY

Jianguo Liu[1,3] and Peter S. Ashton[2]

[1]*Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824-1222 USA*
[2]*Harvard Institute for International Development, and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138 USA*

Abstract. Although the need for implementing ecosystem management across boundaries has been widely recognized, little is known regarding the extent to which loss of species richness resulting from timber harvesting in a focal forest could be offset by the surrounding areas. Using an individual-based, spatially explicit landscape simulation model (FORMOSAIC), which considers not only the dynamics of a focal forest, but also the interactions between the focal forest and the neighboring areas, we found that tree species richness of a tropical forest was related to the interactions between harvest impacts and immigration from adjacent areas. Simulation results indicated that adjacent species-rich forests increased species richness in a focal forest, but neighboring single-species plantations had opposite effects, and these effects were enhanced by the duration of immigration. Heavier harvest impacts on residual trees resulted in lower species richness, although the negative effects were partially offset by immigration from species-rich forests. Immigration after heavy harvest impact led to higher species richness than did immigration before harvesting, when the surroundings were species-rich forests. Harvesting on the edges of a focal forest resulted in higher species richness than harvesting at the center when seed dispersal distances were short, but spatial patterns of harvesting caused no differences in species richness if seeds could disperse into the focal forest from more distant sources. Under the option of no harvest, immigration was more important at small spatial scales than at large spatial scales. From the simulations, we also noticed some unexpected results. For example, heavy harvest impacts reduced a higher percentage of timber species than nontimber species. Simulation results from this study could provide insights into identification of alternative methods for sustainable timber production and conservation of tree species richness beyond natural, management, and ownership boundaries. One potential method would be to establish a species-rich seed zone around a focal forest to partially compensate for negative harvest impacts. Another option would be to harvest timber trees at optimal locations and during optimal periods of time to accommodate dispersal ability and availability of seeds from the surroundings.

Key words: harvest impact; individual-based model; landscape context; landscape mosaics; seed dispersal; seed zone; spatial scales; spatially explicit simulation; species richness; surroundings; tropical forest.

INTRODUCTION

Significant species loss due to timber harvesting is a major threat to sustainable development (e.g., Lubchenco et al. 1991, Panayotou and Ashton 1992). Timber production has been a primary concern of many tropical countries, whereas ecosystem services (Daily 1997) and nontimber goods (e.g., rattan, edible nuts, resins) are usually undervalued. Many regions of Southeast Asia, such as East Malaysia, are now facing severe ecological and socioeconomic consequences because many primary forests either have already disappeared or are declining (Schulte and Schone 1996). Logging activities have been increasing due to improved markets and a larger number of tree species

becoming marketable (Manokaran and Swaine 1994). Although alternative harvesting methods have been suggested to reduce logging impacts, they are often difficult to implement. For example, timber extraction using helicopters or airships causes the least negative impact on residual stands, but it is very expensive (Panayotou and Ashton 1992).

In the past, timber harvesting in East Malaysia was mainly decided by human demands and the size of timber trees inside a forest of interest (Appanah and Weinland 1990). Usually only the most valuable trees were felled, without much consideration of further production (Lamprecht 1989). Species composition and influences of the areas surrounding the harvested forests were basically ignored, although many studies have demonstrated the importance of surrounding areas in determining ecosystem structure and function (e.g., Forman and Moore 1992). For example, the classic

island biogeography theory proposed by MacArthur and Wilson (1967) states that the number of species found on islands is an equilibrium between immigration and extinction rates, and that islands close to a mainland support more species than islands of similar size farther from a mainland. In tropical rain forests, many species in small forest remnants are very sensitive to the vegetation nearby (Lovejoy and Oren 1981, Bierregaard et al. 1992). Also, forest recovery in a disturbed area is inhibited due to the lack of seed dispersal (Buschbacher 1987).

During the past few years, many ecologists and government agencies have recognized the significance of surrounding areas and the need for ecosystem management beyond ecological, political, and ownership boundaries (e.g., Christensen et al. 1996). Ecosystem management requires better understanding of how human disturbances (e.g., timber harvesting) influence ecosystem dynamics and how focal ecosystems interact with adjacent areas. Research on focal ecosystems alone is usually not easy, and study of ecological impacts across boundaries is even more challenging, because more variables must be considered. Interactive effects of the numerous variables involved in studying landscape-scale phenomena (e.g., interactions between seed dispersal from external sources and disturbances occurring inside a focal forest) are difficult to measure through conventional experiments or field observations. Spatially explicit models could provide a useful and complementary tool (e.g., Dunning et al. 1995, Turner et al. 1995a).

Numerous spatially explicit forest models have been developed during the last several decades (e.g., Fries 1974, Ek et al. 1988). Most forest models, however, ignore the characteristics of surrounding areas and their contributions to forest dynamics (Liu and Ashton 1995), even though many seeds in a focal area may come from the surroundings (Jordan 1987) and recruitment is one of the most important factors in plant population dynamics (e.g., Grubb 1977). For example, widely used gap models introduce new individuals to a modeled area from an external, constant seed pool (Botkin et al. 1972, Shugart 1984), regardless of the conditions in the adjacent areas. Although many recent forest models (including some gap models) consider seed dispersal in a spatial fashion (e.g., Urban 1990, Pacala et al. 1993, Clark and Ji 1995), they are limited to simulating seed dispersal within focal forests, whereas spatial interactions through seed dispersal between the focal forests and the surrounding areas are not explicitly modeled. This assumption needs to be reexamined, simply because adjacent nonforest areas (e.g., industrial or agricultural land) cannot provide any seeds to a focal forest (unless seeds from more distant sources are dispersed to the focal forest by wind). At the other extreme, some models (e.g., Pacala et al. 1993) assume that all the seeds are 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). Sometimes the wraparound approach is not a limitation if the modeled landscape is large relative to the spatial heterogeneity of interest. However, it is inappropriate when the surrounding areas differ dramatically from the focal landscape and/or when the focal landscape is so large that seeds on one end cannot reach another end of the landscape.

Although species richness in some tropical forests is among the highest on Earth, and forests in the tropical regions occupy 51.5% of the world's forested area (Borota 1991), relatively few models have been developed for simulating the dynamics of tropical rain forests (see Liu and Ashton 1995 for a review), whereas hundreds of models have been built 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). Furthermore, most of the existing tropical forest models are stand models (e.g., Vanclay 1989), which are mainly used for predicting timber growth/yield, but do not consider the dynamics of species richness.

We developed an individual-based, spatially explicit landscape model (FORMOSAIC) that explicitly treats a focal forest as part of the landscape mosaic (Liu and Ashton 1998). The purpose of this paper is to apply FORMOSAIC in order to simulate the response of species richness in a primary tropical forest of Malaysia to hypothetical timber harvests inside a focal forest, as well as hypothetical immigration from adjacent areas. Specifically, we want to answer the following questions: (1) How do surrounding conditions (e.g., species composition) affect species richness in a focal forest? (2) How does the duration of immigration affect species richness? (3) How do the timing of timber harvesting and the timing of immigration interact to influence species richness? (4) Do varying degrees of harvest impacts on residual trees cause differences in species richness, and can immigration from the surroundings offset the negative harvest impacts on species richness? (5) Do spatial patterns of harvesting change species richness? (6) Do interactions between timber harvest impact and immigration vary across spatial scales?

Methods

Structure and function of FORMOSAIC

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

FORMOSAIC is hierarchically structured at four levels: landscape, focal forest, grid cell, and tree location (Fig. 1). Landscape mosaics consist of a focal
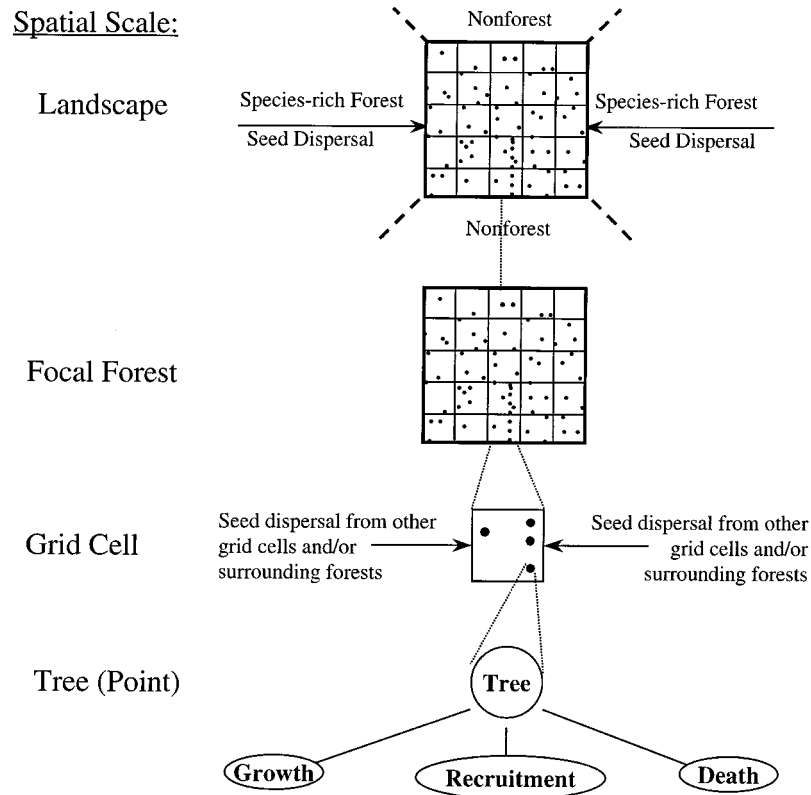
Fig. 1. The hierarchical relationship among four spatial scales (landscape, focal forest, grid cell, and tree location) considered in FORMOSAIC. At the landscape scale, this schematic diagram shows that a focal forest is surrounded by two types of adjacent areas (species-rich forests and nonforests). Seeds can disperse into the focal forest from the adjacent species-rich forests, but no seeds are available from the neighboring nonforests. The focal forest (0.25 ha) is represented by a grid of 25 cells. Each cell is 10 × 10 m and contains many individuals of different tree species. Tree locations are mapped at the point level. The model tracks the recruitment, growth, and death of each individual tree. (Modified from Liu and Ashton 1998.)

forest and surrounding areas. By surrounding areas (SA), we mean the areas outside the focal forest, but within seed dispersal distances. In mathematical terms, $SA = (X + 2D)^2 - X^2$, where X is the side length of a square focal forest and D is the dispersal distance of seeds. Because species may vary in dispersal distances, the surrounding areas for different species may not be the same. Regarding the compositions, there can be a variety of surroundings, such as natural or plantation forests, clearcuts, agricultural fields, industrial land, roads, or residential buildings. In addition, surrounding areas on the four cardinal sides (east, west, north, and south) of a focal forest may each be different. For example, there may be a plantation on the east, a natural forest on the west, a residential area on the north, and agricultural land on the south. Fig. 1 shows a case in which there are species-rich forests on the east and west sides of a focal forest, and nonforests on the north and south sides. Seeds can disperse to the focal forest from adjacent forests, but no seeds are available from the nonforest areas.

A focal forest is represented in the model as a grid of 10 × 10 m cells, each of which contains many in-dividuals of different species. For example, in each 100 m² area of the Pasoh Forest plot in Malaysia (Manokaran et al. 1990), there are usually 60–80 individual trees of ≥1 cm dbh (diameter at breast height) belonging to 30–50 tree species (J. Liu, *unpublished data*). In Fig. 1, the example focal forest is 0.25 ha and is divided into 25 grid cells. In the model, 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 the focal forest. At the tree level, the location (*x*- and *y*-coordinates) of each tree is explicitly mapped. FORMO-SAIC tracks the recruitment, growth, and death of each individual tree.

The data for parameterizing FORMOSAIC were mainly from a 50-ha long-term study plot established in 1985 in the Pasoh Forest Reserve (2°59′ N, 102°18′ E), Peninsular Malaysia (Manokaran et al. 1990, LaFrankie 1992*a*, *b*). The reserve is a lowland dipterocarp forest (Symington 1943). The plot was censused in 1987 and again in 1990. In the first census, the plot

had >800 tree species and >330 000 trees with dbh ≥1.0 cm. All trees were mapped and tagged and their *x*- and *y*-coordinates were 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. Elevation and slope were estimated on a 20 × 20 m basis (i.e., all trees within a 20 × 20 m area were assumed to share the same elevation and slope). Habitat was measured as the distance of each individual tree from the boundaries of swamps or streams.

Liu and Ashton (1998) detailed FORMOSAIC's recruitment, growth, and mortality functions and parameters, based on empirical data from the 50-ha permanent plot. Because sample sizes in the mortality and recruitment analyses for a single species were usually small, we grouped species into four guilds: emergent, canopy, understory, and successional species. The guild 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*). All species of the same guild used the same mortality and recruitment functions. In the growth analysis, we also classified rare species (<1 individual/ha) into the four guilds and developed a growth function for each guild. All rare species in the same guild shared the same growth function. For the 502 species that were abundant (≥1 individual/ha), we developed a growth function for each species. The growth rate of each individual tree was a function of tree size, neighborhood pressure, and local environmental conditions (elevation, slope, and distance from swamps and streams). Neighborhood pressure on a focal tree was measured as the total basal area of all trees except the focal individual in a grid cell. To simplify computations, shading between grid cells was not considered, nor was shading between the focal forest and the surrounding landscape. We assumed that the overcounted shading pressure on the focal individual from within the grid cell was equal to the undercounted pressure from the neighboring grid cells. This assumption was based on the fact that some trees within the same grid cell may not exert shading pressure on the focal tree, but a number of trees in the neighboring cells may compete with the focal tree for light.

For mortality estimation, we classified trees of each guild into four size categories: 1–5 cm, 5–10 cm, 10–30 cm, and >30 cm dbh. 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 size class (>30 cm dbh) did not demonstrate any relationship between mortality rate and tree density or basal area, we used the average mortality value instead of a mortality function in FORMOSAIC.

Analysis of the 50-ha census data indicated that the numbers of new recruits in the 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, we used the average recruitment rate for this guild. In FORMOSAIC, we assumed that recruits could be generated from inside a focal forest and/or from its adjacent areas. A species in the surroundings with a higher population size was assumed to have a higher probability of providing seeds to the focal forest than a species with lower population (Liu and Ashton 1998). The number of seeds dispersed to a given grid cell was a function of seed dispersal ability, distance of the grid cell from the seed source area, availability of seeds in the seed source area, and the maximum number of recruits allowed in the grid cell due to competitive effects. Generally speaking, a grid cell near boundaries of the focal forest would tend to have more immigrants from outside, whereas recruits near the center of the focal forest would come mostly from within the forest. The seed locations in a grid cell were assumed to be random. Because only trees ≥1 cm in dbh were recorded in the 50-ha Pasoh plot, FORMOSAIC accounted for only "effective seeds," which could become seedlings of ≥1 cm dbh.

Dispersal distances were estimated from the census data in the 50-ha permanent plot, according to the locations of adult trees and recruits. For the sake of simplicity, we assumed that recruits were produced by the nearest adult trees of the same species. From this, we obtained a dispersal frequency curve (number of recruits vs. distances from the parent trees) for each species. Because many species did not have a sufficient number of recruits from the census data, we grouped these species into the four guilds discussed earlier. Thus, a dispersal frequency curve for each guild was formed, and a maximum dispersal distance for each guild was derived from the dispersal curve. Considering possible measurement errors in the field, we chose the 95th percentile of the maximum dispersal distance as the nominal dispersal distance. Nominal dispersal distances for emergent, canopy, successional, and understory tree species were 130, 100, 80, and 90 m, respectively. (All species in the same guild were assumed to have the same nominal dispersal distance.)

Because FORMOSAIC is based on individuals, it records information for each individual tree (e.g., species name, size, and location) until the individual dies, matches the species' name with a 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.

Half of the census data (1987 and 1991) from the 50-ha plot were used for model development. The other half of the data were reserved for model validation. Using the 1987 data as initial input and running the model for the same length of time as that between the two censuses, the simulation results from FORMO-
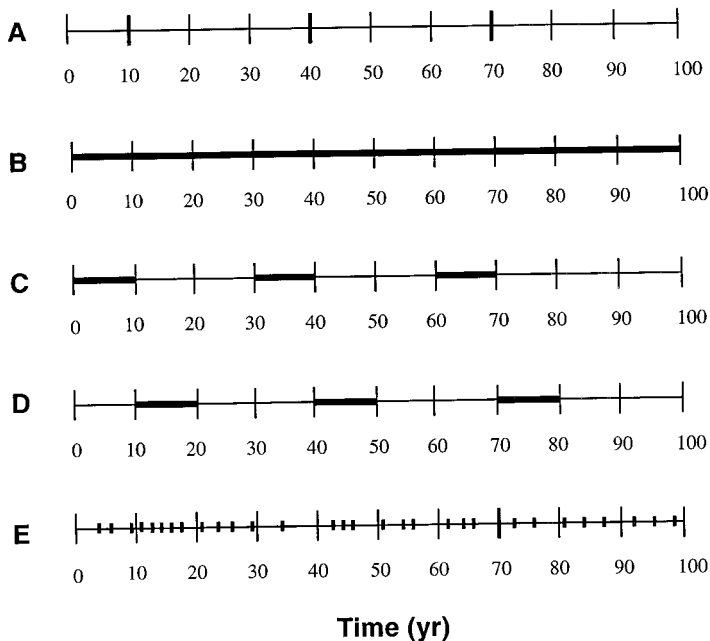
FIG. 2. The timing of harvest in a focal forest and the timing of immigration from adjacent areas to the focal forest. (A) Harvesting at years 10, 40, and 70; (B) immigration every year (continuous immigration); (C) immigration for 10 yr before each harvest; (D) immigration for 10 yr after each harvest; and (E) immigration for 30 yr randomly.

SAIC 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 (the spatial unit for calculation or simulation), P values (from paired t tests) for mean species richness, number of trees, 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. It should be pointed out that the time period between the first census in 1987 and the second census in 1991 is relatively short for the purpose of gauging how well the model matches reality. Therefore, the model should be further tested when new data, such as those from the third census of the Pasoh Forest plot taken in 1996, become available.

Sensitivity analysis indicated that species richness, species composition, and the number of trees in a focal forest were very sensitive to timber harvesting in the focal forest and immigration from adjacent areas (Liu and Ashton 1998). In this study, our purpose was to evaluate the interactive effects of timber harvesting in a focal forest and immigration from the surrounding areas on tree species richness of the focal forest.

Simulation scenarios

To answer the six questions raised in the *Introduction,* we designed a total of 63 different simulations. Any two simulations might differ in one or more factors, including type of surroundings, duration of immigration from the surrounding areas, timing of immigration, degree of harvest impacts on residual trees, harvest locations, seed dispersal distances, and spatial scales of a focal forest.

Harvest impacts.—There were 30 dipterocarp and 90 nondipterocarp timber species in the 50-ha plot (Appanah and Weinland 1993). The family Dipterocarpaceae has ~170 species in 10 genera in Peninsular Malaysia. Dipterocarps are resinous, often huge, trees (Symington 1943). Nondipterocarp timber species are those that can reach timber size, but are members of families other than Dipterocarpaceae (Wyatt-Smith 1952). Dipterocarps are the most important commercial timber species in Malaysia (Appanah and Weinland 1990). As demand for timber products grows, however, many nondipterocarps are also being used for timber production (Manokaran and Swaine 1994). Dipterocarps and nondipterocarps are usually harvested at a minimum size of 50 and 45 cm dbh, respectively (Appanah and Weinland 1990). In our simulations, we followed this criterion to determine which timber trees were eligible for harvesting. Rotation length was assumed to be 30 yr, with the first harvest at year 10 (Fig. 2). Our harvest strategy can be classified as selective cutting, because only timber trees of ≥45 cm dbh were harvested. Unless otherwise indicated, all eligible timber trees were cut across an entire focal forest.

Timber logging can have significant impacts on residual trees (Whitmore 1984, Schaetzl et al. 1989) because of tree fall, road construction, and machinery movement. For the sake of simplicity, we assumed that a harvested tree fell randomly along one of the four cardinal directions (north, south, east, or west). We further assumed that an impact zone (IZ) was positively related to the size of a felled tree (IZ = LZ × WZ), where LZ is the length of the impact zone, LZ = L × H (where L is a changeable parameter ≥0, and H is

TABLE 1. Degree of logging impacts on residual trees. W and L are parameters that determine the area impacted by a felled tree.

Degree of impact	Parameters		
	W	L	P
Heavy impact	2	2	80
Moderate impact	1	1	40
No impact	0	0	0

Note: W represents the effect of crown radius on the width of the impact area; *L* represents the effect of tree height on the length of the impact area; and *P* is the percentage of smaller trees destroyed by a felled tree.

the height of a felled tree); WZ is the width of the impact zone, $WZ = W \times C$ (where W is a parameter with a changeable value ≥ 0, and C is the crown radius of a felled tree). Within an impact zone, a percentage (P) of the trees smaller than the felled trees was destroyed. We did not separate the impacts of road construction and machinery movement from impacts of felled trees. Instead, to simplify computations, we incorporated the impacts of road construction and machinery movement into the model by increasing the size of impact zones and/or the percentage of smaller trees destroyed. To accommodate this, we could vary the values of $P, L,$ and/or W to simulate different degrees of logging impact on species richness in a focal forest (see examples in Table 1).

We ran simulations using three different degrees of logging impact on the residual trees: heavy impact, moderate impact, and no impact (Table 1). Under the no impact scenario, only eligible timber trees were taken out and no other trees were killed. In the moderate impact condition, parameters L and C were set to 1, and thus the impact zone was $H \times C$ (height $\times$ crown radius of a logged tree). Within the impact zone, 40% (P) of the smaller trees were assumed to be killed. Under heavy harvest impact, both L and W were set at 2. The size of the impact zone was then $(2 \times H) \times (2 \times C) = 4 \times H \times C$. We further assumed that 80% (P) of the smaller trees within the impact zone were killed. The two impact scenarios may be similar to selective logging (Appanah and Weinland 1990). The heavy impact scenario might occur when powerful machinery such as crawler tractors is used, whereas the moderate impact scenario may correspond to the case in which winch-powered ground-cable systems are employed for timber logging (Panayotou and Ashton 1992).

Surroundings.—To evaluate the impact of surroundings on species richness in a focal forest, we created six hypothetical types of surroundings: (1) species-rich forests on all four cardinal sides of a focal forest, (2) single-species plantations on all four sides, (3) nonforests on all four sides, (4) nonforests on the north side and species-rich forests on the remaining three sides, (5) nonforests on the north and west sides and species-rich forests on the other two sides, and (6) nonforests on the north, west, and south sides, and a spe-

cies-rich forest on the east side. In this study, a species-rich forest was defined as a forest with the same species richness and composition as the 50-ha Pasoh plot, which had >800 tree species (LaFrankie 1992*a*). In some tropical forested regions, there are many single-species plantations for timber production (Lamprecht 1989). In our simulations, we assumed that the single-species plantations were *Shorea leprosula* (a dipterocarp timber species native to the Pasoh Forest and common in the 50-ha plot). We further assumed that a focal forest could receive seeds from the adjacent species-rich forests or single-species plantations, but not from nonforest areas (e.g., agricultural fields or industrial land).

Duration and timing of immigration.—The surroundings of a focal forest may change in composition and function temporally. For example, adult trees in the surroundings may be destroyed by disturbances (e.g., fires, hurricanes, or windthrows) and, therefore, will be unable to provide seeds to the focal forest for some years to come. Or, an adjacent forest patch may be in an early stage of the natural growth cycle in which it cannot produce seeds (Whitmore 1984). According to Janzen (1978), many tropical species can produce seeds every year, whereas some other species produce seeds at only 120-yr intervals. Between these two extremes, there are many seeding patterns. Because of different seeding features in the surrounding areas, we assumed that seed dispersal took place continuously, periodically, or randomly.

In this paper, we used duration and timing of immigration as surrogates to represent species composition change in the surroundings. Duration of immigration referred to the number of years that the immigrating recruits occurred in the focal forest, whereas timing of immigration indicated in which years the immigrating recruits occurred in the focal forest. Immigrating recruits were those seedlings ≥ 1 cm in dbh that generated from the seeds dispersed from the surroundings to the focal forest. In our simulations, the duration of immigration was 0, 30, 60, or 100 yr. When the total length of immigration was 30 yr, immigration took place for 10 yr before each harvest, for 10 yr after each harvest, or randomly (Fig. 2).

It should be pointed out that, because our census data recorded only trees of ≥ 1 cm dbh, there was no information about how long a seed took to become a seedling of 1 cm dbh, or about the survivorship of seeds and seedlings <1 cm. All the recruitment analyses for the model were done using seedlings ≥ 1 cm dbh. Therefore, "immigration" at year T in our simulations referred to the establishment of seedlings ≥ 1 cm dbh at year $T,$ but the seeds were originally from the surrounding areas at year $T - Y$ (where $Y > 0$ years; Y is the time that external seeds take to become seedlings ≥ 1 cm dbh in the focal forest; the actual Y value would depend on species type and environmental conditions in the focal forest). Similarly, "reproduction" at year

T referred to the establishment of seedlings (≥ 1 cm dbh) whose seeds were produced inside the focal forest at year $T - X$ (where $X \geq 0$ years; X is the time that internal seeds take to become seedlings ≥ 1 cm dbh in the focal forest). The X value might not be the same as the Y value because species types and locations of seeds in the focal forest might differ.

Spatial scales.—Because forest management differs in spatial scales, we ran simulations at five spatial scales: 0.25 ha (50 × 50 m), 1 ha (100 × 100 m), 4 ha (200 × 200 m), 9 ha (300 × 300 m), and 25 ha (500 × 500 m). All of the simulated areas were squares, so that we would avoid shape effects. Most simulations were done at the scale of 0.25 ha, for three major reasons: (1) the area affected by cutting down a single timber tree through selective harvesting is usually small (Appanah and Weinland 1990); (2) many forest patches in human-dominated landscapes are also small (Schelhas and Greenberg 1996); and (3) computations were the most efficient when the scale was 0.25 ha (our simulations were run on Sun Ultra2 and Sun Sparc20 workstations).

Spatial patterns of harvesting and seed dispersal distances.—In some simulations with a 25-ha focal forest, eligible timber trees were cut in an area of 16 ha. The harvested area was either at the center (Fig. 3A) or on the edges (Fig. 3B). To assess the impacts of seed dispersal ability, we set three levels of dispersal distances for each of the four guilds: the nominal dispersal distance, 20% × nominal dispersal distance, and 500% × nominal dispersal distance. Dispersal distances of seeds may vary in response to types of dispersal agents, such as wind, animals, and water (Murray 1986). In many cases, wind and water may carry seeds far away from their parent trees, whereas dispersal by animals may be over more limited distances. We designed the option of 500% × nominal dispersal distance to mimic wind dispersal, and used the scenario of 20% × nominal dispersal distance to simulate cases which there is limited or no seed dispersal.

Data for simulation initialization

To initialize a simulation, we used the environmental data (slope, elevation, and distance from streams and swamps) taken from the 50-ha plot in the Pasoh Forest (0–1000 m from west to east and 0–500 m from south to north); tree data (including tree size, location, and species) were obtained from the 1987 census. For example, a simulated area of 50 × 50 m employed environmental and tree information on a 0.25-ha area (0–50 m from west to east; 0–50 m from south to north) of the 50-ha plot. Similarly, a simulated area of 500 × 500 m used information from a 25-ha area (0–500 m, west to east; 0–500 m, south to north) of the 50-ha plot. In our simulations, a focal forest could be harvested and was assumed to be embedded in one of the six types of surroundings discussed earlier, although the 50-ha study plot in the Pasoh Forest has never been
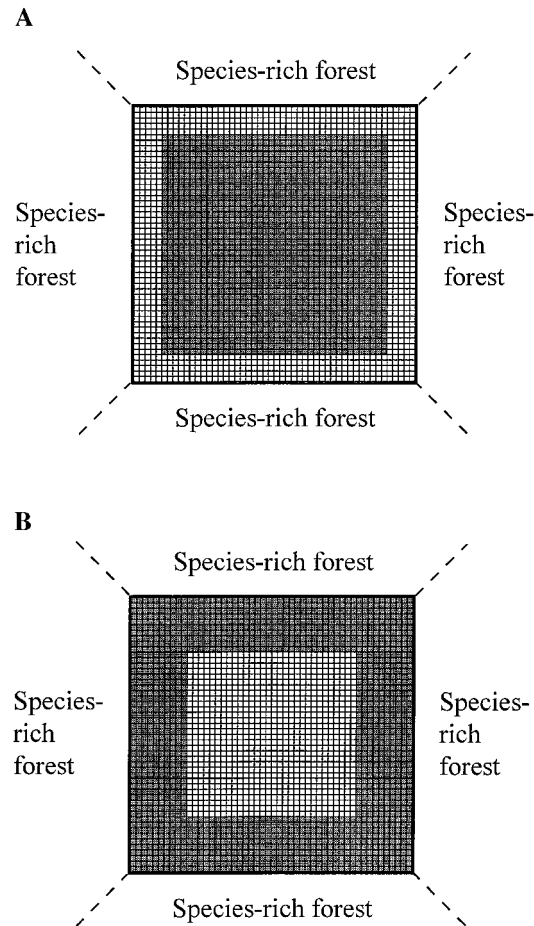

FIG. 3. Spatial patterns of harvesting (shaded area). Eligible timber trees were harvested within an area of 16 ha at the center (A) or on the edges (B) of the 25-ha forest. The 25-ha forest was surrounded by species-rich forests.

harvested and is next to similar species-rich forests. The main purpose of this study was to simulate the changes in species richness in a forest similar to the 50-ha plot, in response to the interactions between timber harvest impacts and various types of surroundings.

Calculation of average species richness and statistical tests

Each simulation step was 1 yr, and each simulation run lasted 100 yr. Each simulation at scales of ≥ 9 ha had five replicates. Simulations at scales of <9 ha had 10 replicates because of a higher variation among replicates. We calculated the average species richness over the entire simulation period (100 yr) and across replicates. To detect main and interactive effects of variables on species richness, and to test for significance of differences in average species richness among various simulation scenarios, we used ANOVA and Bonferroni tests for multiple comparisons in SYSTAT (SPSS 1996). Differences in percentage change in the

TABLE 2. ANOVA for the main and interactive effects of surroundings and immigration on species richness in a 0.25-ha forest. In the simulations, there were three types of surroundings (species-rich forests, single-species plantations, and nonforests) under continuous or no immigration. No timber trees were harvested.

Source	SS	df	MS	F ratio	P
Surroundings	15 712.58	2	7856.29	381.05	<0.001
Immigration	4 082.91	1	4082.91	198.04	<0.001
Surroundings × immigration	16 272.87	2	8136.44	394.65	<0.001
Error	1 113.32	54	20.62		

number of timber and nontimber species were examined with a test for binomial proportions (Ott 1988).

SIMULATION RESULTS

Results are presented in the order of the six questions raised in the *Introduction.*

Type of surroundings and immigration.—There were significant effects of surroundings, immigration, and their interactions on species richness (Table 2). As expected, species richness was higher in a 0.25-ha focal forest surrounded by species-rich forests than in one surrounded by single-species plantations (*Shorea leprosula*) when there was continuous immigration from the surroundings (Fig. 4). Even nonforest surroundings (no seeds dispersed to the focal forest from the nonforests) resulted in higher species richness than did single-species plantations with continuous immigration. When the surroundings provided no immigrants for the focal forest, surrounding types (species-rich forests, single-species plantations, or nonforests) had no effect on species richness (Fig. 4).

The species richness of the focal forest varied in response to changes in the composition of the surrounding areas. As shown in Fig. 5, species richness (Y) decreased as the number of sides next to nonforests (X_1) increased ($Y = 296.86 - 27.93X_1$, $r = -0.95$, $n = 5$). Conversely, species richness increased as the number of sides next to species-rich forests (X_2) increased ($Y = 185.13 + 27.93X_2$, $r = 0.95$, $n = 5$).

The species composition in the focal forest also changed as a result of immigration from the surroundings. For example, when the surrounding forest was Shorea plantations, the percentage of *Shorea leprosula* individuals in the focal forest increased from ~2% at year 1 to 14% at year 100 (Fig. 6). However, when the surrounding forest was a species-rich forest similar to the 50-ha study plot, the *Shorea leprosula* population remained at almost the same proportion (~2%) over the period of 100 simulation years (Fig. 6).

Duration of immigration.—When the focal forest was surrounded by species-rich forests, a longer period of immigration (X_1) increased species richness (Y) in the focal forest (Fig. 7) ($Y = 253.16 + 0.60X_1$, $r = 0.98$, $n = 4$). Under the surroundings of a single-species plantation, however, a longer immigration period (X_2) reduced species richness in the focal forest ($Y = 246.85 - 0.11X_2$, $r = -0.97$, $n = 4$) (Fig. 7). Slopes of the regression equations indicated that species richness was more sensitive to the duration of immigration from the species-rich surroundings than to the duration of immigration from single-species plantation surroundings.

Timing of immigration and harvesting.—There were significant effects of timing of immigration, harvesting, and their interactions on species richness (Table 3). Under heavy harvest impacts, immigration after timber harvesting resulted in the highest species richness (Fig. 8), whereas immigration before harvesting led to the lowest species richness, and immigration in a random order produced intermediate species richness. Under

FIG. 4. Effects of types of surroundings (species-rich forests, single-species plantations, and nonforest) on species richness in a 0.25-ha focal forest. In the simulations, timber trees were not harvested. Results are means ± 1 SE ($n = 10$) for 100-yr simulations under continuous immigration vs. no immigration. If two numbers have different letters (a, b, c), they are significantly different at the 1% level.
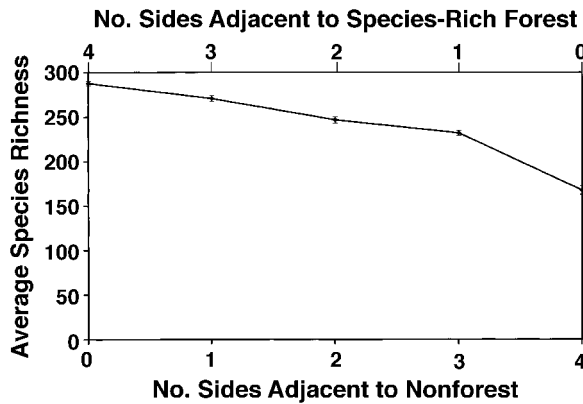
No. Sides Adjacent to Species-Rich Forest
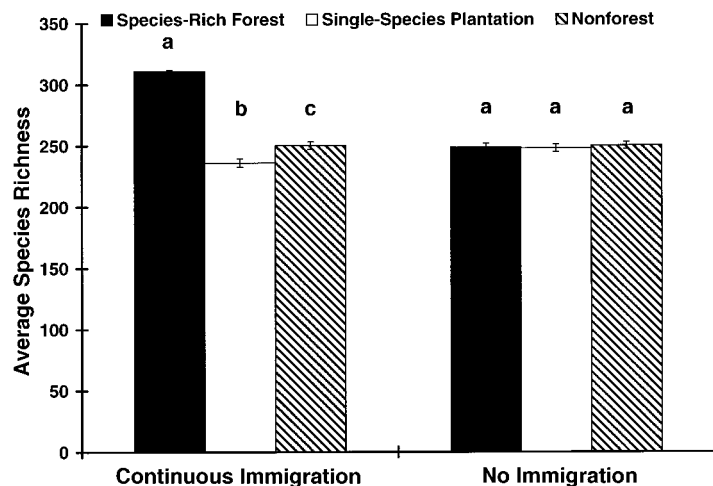
FIG. 5. Relationship between average species richness and the number of sides of a 0.25-ha forest next to species-rich forests and nonforests (mixed types of surroundings). Simulation conditions were heavy harvest impacts and 100 years of immigration. Results are means ± 1 SE ($n = 10$) for 100-yr simulations.

the moderate-impact scenario, random immigration yielded lower species richness than immigration before or after harvesting. Under the scenario of no logging impact, the timing of immigration had no effect on species richness (Fig. 8).

Harvest impacts and compensatory effects of immigration.—Species richness was significantly affected by harvest impact, duration of immigration, and their interactions (Table 4). Under 100 years of immigration, there was no significant difference in species richness among harvesting with moderate impact, harvesting with no impact, and no harvesting with no impact scenarios (Fig. 9). However, heavy harvest impact produced lower species richness than the other three impact scenarios. Under 0 or 30 years of immigration, heavy impact still yielded lower species richness than the other three impact options, and moderate impact resulted in lower species richness than harvesting with no impact or no harvesting with no impact. Surprisingly, however, regardless of the duration of immigra-

tion, species richness was always slightly higher under harvesting with no impact than under no harvesting with no impact, although the difference was not statistically significant for a particular duration of immigration (Fig. 9).

The dynamics of species richness under heavy logging impacts depended upon the availability of immigrants (Fig. 10). Immediately after the first harvest, the number of species was sharply reduced. Species richness was almost fully restored after 30 years with immigration, when the next harvest took place. Subsequent harvests did not reduce species richness as much, because there were not many eligible timber trees available for harvesting. Before the first harvest, species richness increased under continuous immigration, but decreased under no immigration. After the dramatic reduction from the first harvest, species richness gradually recovered when immigration was available, but continued to decline if no immigration occurred.

Under heavy logging impact without immigration, more than half of the dipterocarp timber species (56%) and nontimber species (55%) and nearly three-fourths (73%) of nondipterocarp timber species were lost by the end of 100 simulation years (Table 5). Combining both dipterocarp and nondipterocarp timber species, about two-thirds (66%) of timber species disappeared. With continuous immigration, heavy logging impact reduced the number of species in nondipterocarp timber species and nontimber species only slightly, and the number of dipterocarp species actually increased by ~4%.

Spatial patterns of harvesting.—Harvest locations, dispersal distances, and their interactions all had significant effects on species richness (Table 6). Under nominal or reduced dispersal distance, harvesting eligible timber trees on the forest edges led to higher species richness than harvesting at the forest's center (Table 7). Using 500% of the nominal dispersal distance, however, harvest locations did not generate sig-
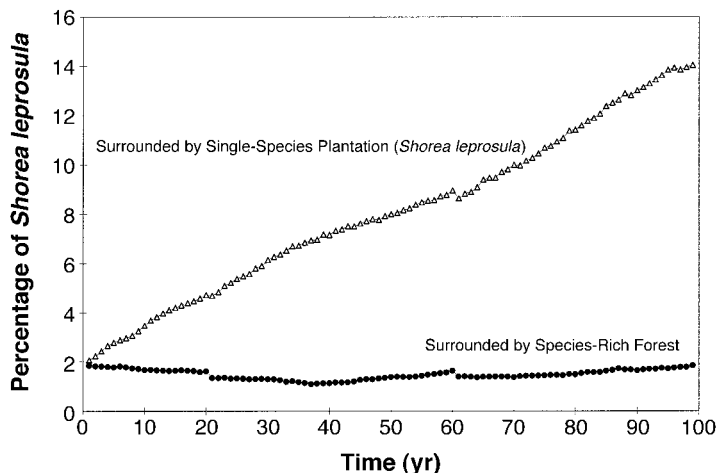

FIG. 6. Change in the percentage of a dipterocarp timber species (*Shorea leprosula*) in a 0.25-ha focal forest. When the focal forest was surrounded by single-species plantations (*S. leprosula*), the percentage of *S. leprosula* gradually increased from ~2% to 14% over a period of 100 simulation years. When the focal forest was located next to species-rich forests like the 50-ha study plot in the Pasoh Forest, however, the percentage of *S. leprosula* remained quite stable. In the simulations, timber trees were not harvested, and the duration of immigration was 100 yr. Results are means ($n = 10$) for 100-yr simulations.

FIG. 7. Relationship between average species richness and the duration of immigration to a 0.25-ha focal forest from two types of surroundings (species-rich forests and single-species plantations). When the duration of immigration was 30 or 60 yr, immigration took place at random years. In the simulations, timber trees were not harvested. Results are means ($n = 10$) for 100-yr simulations.
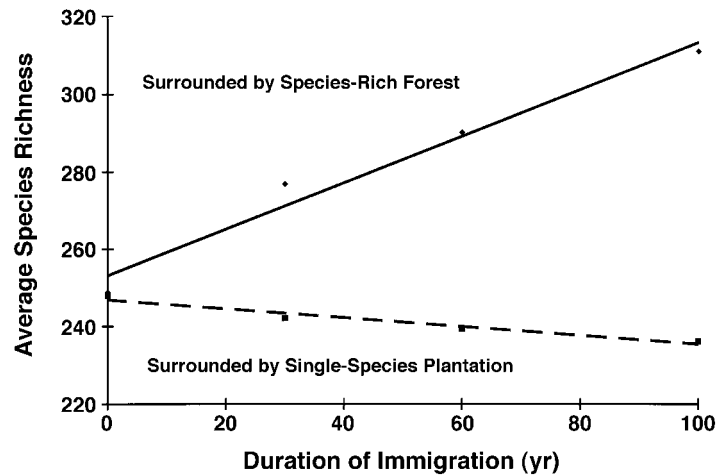
nificant differences in species richness. When dispersal distance was 20% of the nominal dispersal distance, species richness was reduced when harvesting took place on the forest edges. Harvesting at the center did not produce a significant difference in species richness, despite reduction in seed dispersal distance. When the seed dispersal distance was set at 500% × nominal dispersal distance, the average number of species was much greater than that with the nominal or reduced dispersal distance.

Spatial scales.—As spatial scales of simulated forests increased from 0.25 ha to 25 ha, average species richness increased (Fig. 11A). Under no harvest impact (Fig. 11B), the difference in species richness between continuous immigration and no immigration was small. At scales ≥9 ha, immigration did not affect species richness. Under heavy harvest impact (Fig. 11B), however, the difference in species richness between continuous immigration and no immigration increased, reached a peak, and then decreased along a spatial scale. The peak of the difference in species richness occurred at the scale of 1 ha. Even at the scale of 25 ha the difference was still significant. At the same spatial scale, the difference in species richness between continuous immigration and no immigration was much greater under heavy harvest impact than under conditions of no harvest.

DISCUSSION AND CONCLUSIONS

It is obvious that both timber harvesting and surroundings played an important role in influencing tree species richness, and the interactions between harvest impact and immigration from the adjacent areas were quite complex. Some of the results were unexpected and surprising. For example, heavy harvest impact damaged a higher percentage of timber species than nontimber species. The loss of a higher percentage of timber species might be related to their higher local extinction rate (J. Liu, *unpublished data*). Given the conditions of no harvest impact and no immigration, timber species decreased by 41.36%, whereas nontimber species decreased by 30.04%. Under the scenario of harvest impact and no immigration, however, timber species and nontimber species decreased by 66.32% and 54.67%, respectively (Table 5). In other words, harvest impact caused ~25% more loss to both timber and nontimber species. These simulation results indicated that immigration was more important for maintaining long-term timber species richness than for retaining nontimber species richness, regardless of harvest impact. Therefore, it is necessary to incorporate information about the surrounding conditions into sustainable timber management policies.

Some of our simulation results can be explained by

TABLE 3. ANOVA for the main and interactive effects of the timing of immigration and harvest impact on average species richness in a 0.25-ha focal forest surrounded by species-rich forests. The duration of immigration was 30 yr.

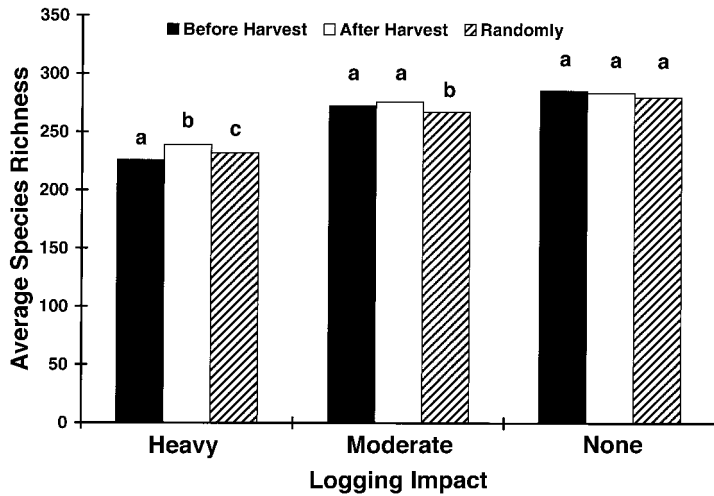| Source	SS	df	MS	F ratio	P
Timing of immigration	658.93	2	329.46	40.41	<0.001
Harvest impact	43 690.11	2	21 845.05	2679.17	<0.001
Timing of immigration × harvest impact	694.94	4	173.73	21.30	<0.001
Error	660.44	81	8.15		

Fig. 8. Impacts of the timing of immigration on species richness in a 0.25-ha forest surrounded by species-rich forests. The duration of immigration was 30 yr. If two numbers have different letters (a, b, c), they are significantly different at the 1% level. Results are means ± 1 SE ($n = 10$) for 100-yr simulations.

the intermediate disturbance hypothesis (Connell 1979), island biogeography theory (MacArthur and Wilson 1967), or the source–sink hypothesis (e.g., Pulliam 1988). Timber harvesting is a major human-induced disturbance in many forests (e.g., Schelhas and Greenberg 1996), including the tropical forest that we studied (Panayotou and Ashton 1992, Manokaran and Swaine 1994). Simulation results indicate that the consequences of timber harvesting seem to be consistent with the intermediate disturbance hypothesis, which states that intermediate disturbances result in the highest species diversity. Under the scenario of logging with no impact, species richness did not differ statistically from that under the scenario of no logging (Fig. 9); however, logging without impact always produced slightly higher species richness than no logging and no impact. Therefore, in our simulations, the equivalent of an "intermediate disturbance" (Connell 1979) might be harvesting eligible timber trees without impacting residual timber trees.

The surroundings of a focal forest in our simulations may be similar to the "mainland" of the island biogeography theory (MacArthur and Wilson 1967), or to the "source habitat" of the source–sink hypothesis (e.g., Pulliam 1988). In an "island" or "sink habitat," some species become extinct without a supply of immigrants from the "mainland" or "source habitat." Our simulation results are consistent with the conclu-

sions from island biogeography theory: without immigration, species richness of focal forests at small spatial scales dropped significantly. At large spatial scales (≥9 ha), however, immigration did not affect species richness if there was no harvest impact (Fig. 11).

Species with different habitat needs responded to timber harvests differently. In the 1987 census of the 50-ha Pasoh Forest plot, there were 403 understory tree species (~50% of all tree species), 279 canopy species (~34%), 79 successional species (~10%), and 48 emergent species (~6%). These various guilds have different light requirements. Understory species are shade-tolerant, whereas successional species are light-demanding, with emergent and canopy species being somewhere between the two extremes (Whitmore 1984). As a result, different types of species had different responses to timber harvests in our simulations. For example, in a 0.25-ha forest under continuous immigration and heavy logging impact, the successional guild had an increase of about four species (~16% increase), whereas the three other guilds suffered significant decreases in species numbers compared with those under continuous immigration and no logging impact (Table 8). We believe that this was because heavy logging impact created large openings, thus allowing more light and generating good habitats for successional species.

TABLE 4. ANOVA for the main and interactive effects of harvest impact and the duration of immigration on average species richness in a 0.25-ha focal forest surrounded by species-rich forests. When the duration of immigration was 30 yr, immigration recruits (≥1 cm in dbh) established themselves in the focal forest at random years.

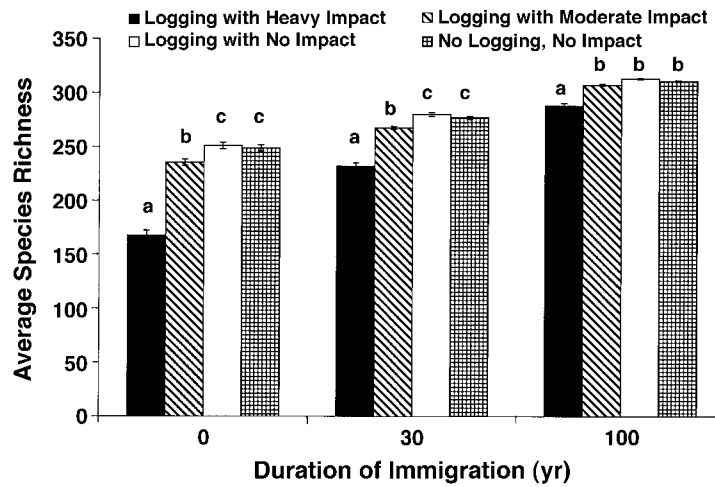| Source	SS	df	MS	F ratio	P
Harvest impact	54 767.46	3	18 255.82	1287.61	<0.001
Immigration duration	125 314.09	2	62 657.04	375.16	<0.001
Harvest impact × immigration duration	12 070.61	6	2 011.76	41.34	<0.001
Error	5 255.42	108	48.66		

FIG. 9. Interactive effects of logging impact and the duration of immigration on average species richness in a 0.25-ha focal forest surrounded by species-rich forests. When the duration of immigration was 30 yr, immigration took place at random years. If two numbers have different letters (a, b, c), they are significantly different at the 1% level. Results are means ± 1 SE ($n = 10$) for 100-yr simulations.

The simulation results from this study have implications for sustainable timber production with conservation of tree species richness. Our simulations showed that heavy logging impact eliminated a higher percentage of timber species than nontimber species (Table 5), but this negative harvest impact on species richness was partially offset by immigrants to the focal forest from adjacent areas (Table 5). Although efforts to reduce logging impacts should continue, an alternative approach would be to harvest timber trees at optimal locations and during optimal time periods, in order to accommodate dispersal ability and increase the availability of seeds from the surroundings. Another alternative would be to set aside certain areas around focal forests as "seed zones." These so-called "seed zones" would provide seeds for areas experiencing heavy or moderate harvest impacts on residual trees.

Based on our simulation results, we propose a few "rules of thumb" for determining an area as a "seed zone" and for harvesting timber trees:

1) Maintain species-rich surroundings. There should be as many species as possible in a seed zone, which should include both timber and nontimber species. Sim-

ulations in this study showed that single-species plantations around a focal forest were worse than a nonforest surrounding (Fig. 4), because the recruits from the single species, once established, excluded some other tree species in the focal forest (Fig. 6).

2) Place species-rich forests around the focal forest on all sides. Our simulation results showed that species richness of a focal forest was positively related to the number of sides near species-rich forests (Fig. 5).

3) Sustain a continuous supply of seeds and, thus, availability of recruits from the species-rich surroundings to the focal forest. As indicated in Fig. 7, a longer period of immigration increased species richness in the focal forest.

4) Consider the timing of harvesting and the timing of immigration carefully if immigration from the adjacent areas is not continuous. Our simulation results demonstrated that immigration after harvesting was best, because harvesting destroyed many existing trees and immigrants (Fig. 8).

5) Harvest eligible timber trees on the edges of the focal forest when seed dispersal distances are short. When harvesting in our simulations took place in the
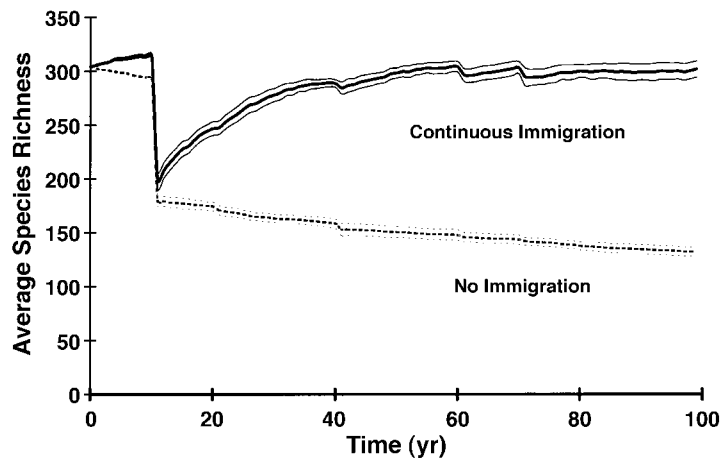

FIG. 10. Dynamics of species richness under heavy harvest impacts with continuous or no immigration. Harvesting took place at years 10, 40, and 70. Reduction in species richness at years 20 and 60 was partly due to windthrows, which could cause some damage to the forest. The focal forest was 0.25-ha and was surrounded by species-rich forests. Results are means ($n = 10$) for 100-yr simulations. Heavy lines indicate mean values, and light lines indicate 95% CI about mean values.

TABLE 5. Percentage change (PC) in the number of timber and nontimber species (mean ± 1 SE) due to heavy harvest impact. PC = $(N_e - N_b)/N_b \times 100\%$, where N_b and N_e are the average number of species at the beginning and the end of simulations, respectively. In the simulations, the focal forest was 0.25 ha, and the surroundings were species-rich forests.

	Timber species			Nontimber species
Immigration	Dipterocarps	Nondipterocarps	All timber species	
No immigration	−56.14 ± 1.34	−73.04 ± 3.86	−66.32 ± 1.70[A, a]	−54.67 ± 1.28[A, b]
Continuous immigration	4.44 ± 3.23	−0.44 ± 4.59	1.05 ± 2.80[B, a]	−1.23 ± 2.56[B, a]

Note: If two numbers are followed by different letters, they are significantly different at the 1% level: letters a and b compare differences in percentage change between timber and nontimber species, for either no immigration or continuous immigration; letters A and B indicate differences in percentage change between no immigration and continuous immigration, for either timber or nontimber species.

center of the focal forest, seeds with limited dispersal ability could not reach the harvested areas and thus species richness was reduced (Table 7).

6) Improve conditions in the harvested areas by scarifying compressed soil and removing dense woody litter so that seeds dispersed from the surrounding areas can easily germinate and become established in the harvested areas.

Although some of these ''rules'' may be hard to follow, it is necessary to conserve species richness in managed forests, because nature reserves alone are not sufficient for conservation (e.g., Hansen et al. 1991).

There are two major differences between the proposed seed zone method and traditional methods of natural regeneration in silvicultural practices (e.g., Nyland 1996). First, the seed zone method explicitly considers the impact of the surroundings on a focal forest, but traditional methods of natural regeneration emphasize the focal forest and ignore the effects of seeds from adjacent areas. Second, the seed zone method attempts to provide seeds of both timber and nontimber species to a focal forest, but traditional silvicultural practices mainly pay attention to timber species. For example, in the seed tree method, only a few seed trees of timber species are left to furnish seeds to restock the cleared area naturally (Smith 1986).

The simulation results in this study may be an optimistic scenario regarding harvesting impacts on tree species richness, because the model assumes that soil in the focal harvested forest offers good conditions for seeds from adjacent areas to germinate and become established. In reality, soil in parts of the harvested forest may be compacted and, therefore, not suitable for seeds dispersing to the focal forest. In the soil of other parts of the harvested forest that are not disturbed or are less disturbed, some undamaged small trees may be more competitive than the seeds from the surrounding areas, because regeneration that was already established before logging dominates succession following logging in most broad-leaved forests (Smith 1986), and larger juveniles have an advantage in regeneration (Brown and Whitmore 1992). Furthermore, regeneration of climax species is scant on soil compressed by machinery, or where woody litter is dense (Whitmore 1984). It takes many years before postfelling recruitment and growth occur under successive vegetation beyond the edge of the residual canopy (e.g., Ashton 1978). In other words, harvest impacts might be more severe than those shown in the simulations, and the role of seed dispersal from adjacent areas might be less important. Nevertheless, the model provides a preliminary approach to estimating impacts of different timber harvesting regimes and surrounding conditions. Moreover, even though our simulations might have underestimated the impacts of timber harvesting on species richness, these simulated impacts are still large enough to warrant serious attention.

As mentioned in the *Methods* section, FORMOSAIC mimics forest dynamics in fragmented and heterogeneous landscape mosaics, which represent a common pattern of forest distribution (Harris 1984, Shugart 1984, Schelhas and Greenberg 1996). Ecological processes and patterns vary at different spatial scales (e.g., Levin 1992, Turner et al. 1995b). FORMOSAIC can

TABLE 6. ANOVA for the main and interactive effects of harvest location and dispersal distance on species richness in a 25-ha forest. Eligible timber trees were harvested within a 16-ha area at the center or edges of the 25-ha forest, under three scenarios of seed dispersal distance (nominal dispersal distance, 20% × nominal dispersal distance, and 500% × nominal dispersal distance).

Source	SS	df	MS	F ratio	P
Harvest location	588.22	1	588.21	54.30	<0.001
Dispersal distance	11 607.69	2	5803.84	535.78	<0.001
Harvest location × dispersal distance	368.51	2	184.25	17.01	<0.001
Error	259.98	24	10.83		

Note: The 25-ha forest was assumed to be surrounded by species-rich forests; other parameters for the simulations were continuous immigration and heavy harvest impact.

TABLE 7. Impact of harvest locations and dispersal distances on species richness (mean ± 1 SE) in a 25-ha forest assumed to be surrounded by species-rich forests. Eligible timber trees were harvested within a 16-ha area at the center or edges of the 25-ha forest under three scenarios of seed dispersal distance. Other parameters for the simulations were continuous immigration and heavy harvest impact.

	Harvest locations	
Dispersal distance scenarios	Center	Edge
Nominal dispersal distance	668.20 ± 3.91[A, a]	684.01 ± 3.48[A, b]
20% × nominal dispersal distance	669.10 ± 3.92[A, a]	680.60 ± 3.52[B, b]
500% × nominal dispersal distance	717.56 ± 2.48[B, a]	716.82 ± 2.44[C, a]

Note: If two numbers are followed by different letters, they are significantly different at the 1% level: letters a, b, and c are used for comparing differences in species richness under two harvest locations for the same dispersal distance; letters A, B, and C indicate differences in species richness under different dispersal distances for the same harvest location.

run simulations at multiple spatial scales and provides a tool to integrate the effects of timber harvesting inside a focal forest with those of immigration from the surroundings of the focal forest. Our simulations indicated that immigration was important for maintaining species richness in a focal forest, especially under heavy harvest impact, although the degree of importance varied among spatial scales (Fig. 11A).

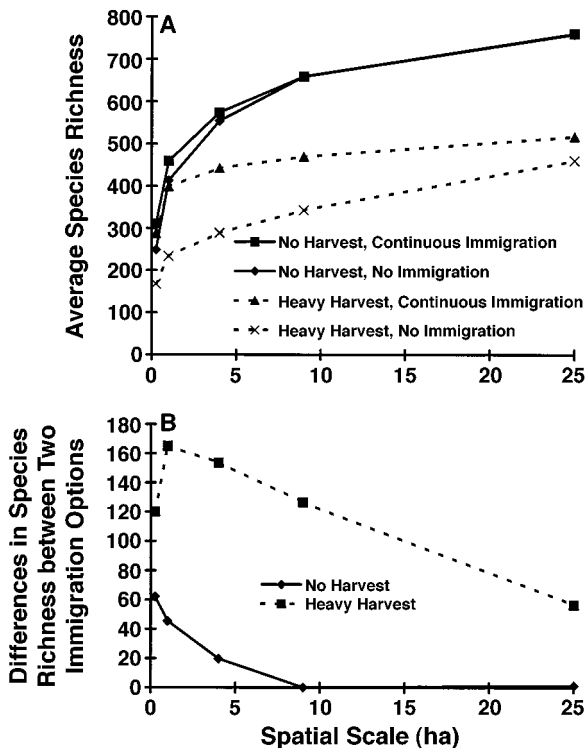We noticed that thresholds existed across spatial

FIG. 11. Effects of spatial scales on average species richness. (A) Species richness under two types of immigration options (continuous immigration vs. no immigration) and two types of harvest impact. (B) Differences in species richness between the two immigration options under no harvest impact vs. heavy impact. Focal forests were surrounded by species-rich forests. Results are means ($n = 10$ for spatial scales of <9 ha and $n = 5$ for spatial scales of ≥9 ha) for 100-yr simulations.

scales (Fig. 11B). Under conditions of no harvest, the differences in species richness of the focal forest between the two immigration options (continuous immigration vs. no immigration) decreased as the focal forest increased in size. When the focal forest was ≥9 ha, no significant difference was found. We observed that the differences in species richness (Y) between the two immigration options were positively related to the ratio of seed zone area to the focal forest area (R_{zf}), $Y = 21.1950 \ln(R_{zf}) - 1.9458$ ($r^2 = 0.96$, $n = 5$, $P < 0.01$). When the ratio was less than 2, the effect was not significant, probably because the number of seeds from the seed zone was not large enough. However, under heavy harvest impact, the differences in species richness between the two immigration options were not related to R_{zf}. Instead they were well described by a linear equation, $Y = 986.42\text{POT} - 333.9$ ($r^2 = 0.95$, $n = 5$, $P < 0.01$), where POT is the potential of the focal forest (after heavy harvest impact) to accept more species from adjacent areas: $\text{POT} = (S_{nc} - S_{hn})/S_{nc}$, where S_{nc} is the number of species under "no harvest, continuous immigration" conditions, and S_{hn} is the number of species under "heavy harvest, no immigration" conditions. The biggest difference in species richness between the two immigration options was at the scale of 1 ha, rather than at the smallest scale (0.25 ha). The reason appears to be that the potential to accept more species from adjacent areas at the scale of 0.25 ha (POT = 0.46) was smaller than that at the scale of 1 ha (POT = 0.49).

Individual-based, spatially explicit models like FORMOSAIC demand large amounts of computational time, but this problem will lessen as computer technologies develop (Levin et al. 1997). Compared to many long-term field observations or experiments, the time to run a simulation can be trivial. However, it is often not easy to obtain adequate data for parameterizing and validating the models. Development of realistic models depends on good data. Thus, serious attention should be paid to data collection, because studying ecological processes and patterns beyond boundaries is more complicated than studying a focal forest alone. In this paper, we used timing and duration

TABLE 8. Change in species composition of a 0.25-ha focal forest under two types of harvest impact. In the simulations, surroundings were species-rich forests, and there was continuous immigration. Letters a and b indicate that the numbers of species in each guild are significantly different (vertically) at the level of $P < 0.01$.

Harvest impact	Number of species in each guild (mean $\pm$ 1 SE)				
	Emergent	Canopy	Understory	Successional	Total
No impact	26.05 ± 0.07[a]	94.49 ± 0.20[a]	171.60 ± 0.25[a]	20.79 ± 0.17[a]	312.93 ± 0.24[a]
Heavy impact	23.39 ± 0.09[b]	87.70 ± 0.41[b]	152.48 ± 0.69[b]	24.22 ± 0.23[b]	287.79 ± 0.39[b]
Rate of change	-10.21%	-7.19%	-11.14%	$+16.49\%$	-8.03%

of immigration as surrogates to represent dynamic change in the surroundings. Model predictability could be enhanced by research on (1) forest dynamics in the adjacent areas, (2) regeneration patterns and processes of seed dispersal from adjacent areas to the focal forest, and (3) survivorship of small seedlings <1 cm in dbh (which were not recorded during the censuses of the 50-ha plot in the Pasoh Forest; Manokaran et al. 1990).

In this case study, we have made an attempt to explicitly address the interactive effects of landscape context and timber harvesting on species richness of a tropical forest. This approach could also be useful for understanding the dynamics of tree species richness in broad-leaved, moist, temperate forests, because there are many similarities (e.g., fragmentation; Harris 1984). Despite the many challenges ahead, simulation study of ecological processes and patterns across natural, ownership, and management boundaries has the potential to provide valuable information for resource management from a landscape perspective.

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