Ecology, 86(6), 2005, pp. 1540–1547

IMPACTS OF NEST CONSTRUCTION BY NATIVE PIGS (*SUS SCROFA*) ON LOWLAND MALAYSIAN RAIN FOREST SAPLINGS

Kalan Ickes,[1,4] Christopher J. Paciorek,[2,5] and Sean C. Thomas[3]

[1]*Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803 USA*
[2]*Department of Statistics, Carnegie Mellon University, Pittsburgh, Pennsylvania 15213 USA*
[3]*Faculty of Forestry, University of Toronto, Toronto, Ontario, M5S 3B3, Canada*

Abstract. Isolation of remnant forest patches, coupled with anthropogenic changes in the surrounding landscape, often leads to changes in the population density of forest-dwelling mammals. At Pasoh Forest Reserve in Peninsular Malaysia, densities of native wild pigs (*Sus scrofa*) are 10–100 times greater than historical levels due to the local extinction of feline predators and the presence of abundant food sources in areas adjacent to the forest. Female pigs build reproductive nests out of understory vegetation; at Pasoh these nests are constructed primarily of woody saplings several meters tall that pigs snap or uproot, causing substantial local damage. We documented the prevalence of nest building by pigs at Pasoh within a 25-ha area from 1995 to 1998 and investigated the impacts of this mammalian behavior on the understory plant community. In total, 643 pig nests were enumerated, providing an estimate that 6.0 nests$\cdot$ha$^{-1}\cdot$yr^{-1} were constructed in the survey area. Pigs avoided constructing nests adjacent to trails but otherwise built nests throughout the 25-ha survey area. A single pig nest contained, on average, 267 $\pm$ 86 (mean $\pm$ 1 SD) woody saplings, of which 45% had been uprooted and 55% had the main stem snapped. The understory area affected by the construction of a single pig nest averaged 244 $\pm$ 112 m^2, with 53% of all free-standing woody plants $\geq$70 cm tall and $<$2.0 cm dbh in this area being uprooted or snapped. As a result of nest building, pigs caused an estimated 29% of the observed tree mortality of saplings 1–2 cm dbh, and 43% of sapling mortality and damage combined. Pigs affected plant families differently, with individuals from the economically and ecologically paramount Dipterocarpaceae being about two times more likely to be used in nest construction than other taxa. Our results indicate that pig nest-building activities are a major source of sapling mortality, and that their effects probably will result in substantial shifts in tree community composition in this forest.

Key words: Dipterocarpaceae; lowland rain forest; Malaysia; pig nests; sapling damage; Sus scrofa; *tree demography; tropical forests.*

Introduction

Mammals affect the demography and distribution of plant species through behaviors, such as mound building or digging, that result in physical disturbance (Platt 1975, Shachak et al. 1991, Tardiff and Stanford 1998). Most often the disturbance occurs on a small spatial scale, with plant composition being altered on, in, or immediately adjacent to the disturbed area. However, in some cases mammals can influence plant dynamics at a community level. In fragmented forest landscapes, anthropogenic changes in and around forest fragments can drastically alter the density of mammals within forest patches, leading indirectly to extensive changes in the plant community. For example, elephants (*Loxodonta africana*) in parts of Africa increased in density at a local scale because logging, forest fragmentation, and fencing forced them to concentrate their foraging in smaller areas. The increase in density resulted in increased tree damage and mortality and retarded forest succession (Jachmann and Croes 1991, Struhsaker 1997). Similarly, at Gunung Palung National Park in Borneo, extensive logging outside the park boundaries changed the foraging behavior of bearded pigs, *Sus barbatus* (Curran and Leighton 2000), which may have caused a precipitous decline in seedling recruitment over a 10-year period (Curran et al. 1999). In the present study, we document another example of negative impacts on plants caused by an elevated population density of a large mammal within a protected forest: namely, the hyperabundance of wild pigs (*Sus scrofa*) in a rain forest reserve in peninsular Malaysia, and the impacts of their nest building on the forest understory plant community.

The native range of *Sus scrofa* extends throughout Europe and continental Asia as far south and east as Peninsular Malaysia, as well as to the islands of Sumatra and Java (Oliver 1993). Throughout their range,

Manuscript received 25 May 2004; revised 8 October 2004; accepted 19 October 2004; final version received 24 November 2004. Corresponding Editor: R. S. Ostfeld.

[4] Present address: 7500 Kirby Drive #1023, Houston, Texas 77030 USA. E-mail: kalan42@hotmail.com

[5] Present address: Department of Biostatistics, Harvard School of Public Health, Boston, Massachusetts 02115 USA.

female pigs seek shelter or construct nest sites shortly before giving birth. The amount and type of material gathered for nest building depends on environmental conditions and availability (Jensen 1989), but in most habitats young are born under dense vegetation such as shrubs or herbaceous plants gathered into a pile. In both cases, the impact on the surrounding vegetation is usually limited. However, nest building may have a profound impact on the understory vegetation in primary lowland rain forest of Pasoh Forest Reserve (PFR) in Peninsular Malaysia for two reasons. First, herbaceous ground cover is sparse at PFR, so female pigs predominately use woody vegetation when building nests. Females grasp 40–350 cm tall saplings in their jaws and twist their head to the side, either snapping the stem or uprooting the sapling entirely. Stems are then arrayed in a radial fashion over a shallow, crater-like depression in the soil, with the foliage in the center and the snapped or uprooted ends facing outward (Medway 1963). More than one individual may work to construct a nest, but on the few occasions when this was observed, the second pig was much smaller, possibly a daughter of the larger pig from a previous birth (K. Ickes, *personal observations*). Pigs use different sizes of woody plants, with larger pigs snapping off or uprooting taller, larger diameter plants. Stems that are uprooted die, but those that are snapped off may resprout from the stump that remains.

The second reason that nest building may have an unusual impact on the plant community at PFR is that wild pigs have increased dramatically in density within the reserve. PFR is only 2500 ha, which is too small to support populations of the natural feline predators of pigs. In addition, PFR is virtually surrounded by extensive African oil palm tree plantations that fruit continuously, providing a tremendous year-round food supply for pigs that live in the forest reserve, but move into the tree plantations to feed. Pig density is 10–100 times the historical levels (Ickes 2001), and there has been a concomitant increase in the number of reproductive nests constructed annually in the forest. The combination of small reserve size, changes in land use in the surrounding matrix, and the high mobility of pigs has created a large-scale edge effect that influences the forest understory throughout the entire reserve (Ickes and Williamson 2000).

Here, we document the incidence of nest building by *Sus scrofa* at Pasoh and quantify the impacts of this behavior on the understory plant community. Specifically, we address the following questions: (1) How many nests are constructed annually at PFR? (2) Are nests spatially clumped or placed preferentially in certain habitats? (3) How many and what sizes of stems are used in nest construction? (4) How large an area is affected around each nest when pigs remove stems for construction material? (5) What proportion of tree mortality at PFR is caused directly by pigs? (6) Are certain species or taxonomic groups at greater risk than others from nest building?

Materials and Methods

Site description and field methods

Fieldwork was conducted from February 1995 to October 1998 at Pasoh Forest Reserve (2°59′ N, 102°18′ E) in Peninsular Malaysia. The reserve consists of a central 650 ha of primary lowland dipterocarp forest, surrounded by 650 ha of regenerating forest selectively logged 45–50 years ago (Okuda et al. 2003). The eastern extent of the reserve contains an additional 650–1000 ha of primary lowland and hill dipterocarp forest. Approximately 85% of the reserve boundary is adjacent to extensive African oil palm (*Elaeis guineensis* Jacq.) plantations. Annual rainfall is ~2000 mm, with a known range of 1700–3200 mm/yr (Kochummen et al. 1990). Monthly rainfall means exceed 100 mm and thus the climate is technically aseasonal; however, there may be consecutive months within a single year with substantially less than 100 mm of rain.

We conducted surveys of pig nests in the western half of a 50-ha (1000 $\times$ 500 m) permanent plot located in the center of the reserve in old-growth forest. The plot was established between 1985 and 1988, and additional surveys that recorded tree diameters, mortality, damage, and recruitment were initiated in 1990, 1995, and 2000. During plot establishment, all trees $\geq$1.0 cm dbh (diameter at breast height) were tagged, identified, measured for dbh, and mapped. The plot is divided into 1250 20 $\times$ 20 m subplots, in 50 columns of 25 subplots aligned north–south, and marked with steel posts at each corner. Each subplot is marked at 5 $\times$ 5 m intervals with small yellow stakes. In order to permanently mark trees $<$5.0 cm in dbh, vinyl ribbon is used to loosely tie tags to the main stem of the sapling, either above a branch near eye-level, or placed at ground level around the stem.

We conducted three surveys of pig nests: (1) February–October 1995, (2) May–October 1996, and (3) May–October 1998. All 20 $\times$ 20 m subplots were searched in 1995, but 48 subplots (1.9 ha) were missed in 1996 and 20 subplots (0.8 ha) were missed in 1998. All pig nests located within this 25-ha area were mapped using the plot coordinate system, estimated to the nearest 1 m from the 5 $\times$ 5 m stakes or mapped to the nearest tree if stakes were missing. In calculating the number of nests constructed per hectare per year, we controlled for any differences in time since particular plots were searched between the pig nest surveys.

We estimated the age of all nests based on the color of the leaves and the extent of decomposition. Three age categories were recognized and determined by the same observer in all three surveys: new, medium, and old. An attempt was made to quantify how long a nest would remain in each age category, but variables such as litterfall, rainfall or humidity, the presence of termite nests nearby, and nest size greatly affected the rate of nest decomposition or visibility and made the age classification system rather subjective. Rough estimates were that a new nest was <2 mo old, medium nests 2–6 mo old, and old nests were created >6 mo prior to discovery. Nests were searched thoroughly for tree tags from snapped or uprooted saplings. The area around each nest was searched for tagged stumps obviously created during nest construction. All tag numbers and the locations were recorded where found, either in the nest or on a stump. For stumps with tags, we recorded mortality, resprouting, and whether or not a pig had removed the main stem or a smaller shoot.

Because tags from the 50-ha plot only provide information about trees ≥1.0 cm dbh, 10 nests were examined in detail to quantify all plants used, including woody stems <1.0 cm dbh. These nests were selected, irrespective of size, if they appeared to be <48 h old when discovered. The fresh condition of the stumps allowed for precise determination of which stumps had been damaged for the construction of the new nest rather than older nests in the area. At each nest all stumps were tagged, mapped, and measured for height and basal diameter (BD). Pigs usually snap saplings 20–60 cm above ground, so it was not possible to measure the dbh of stumps. Instead, dbh was estimated based on stump BD (see *Data analysis*).

The area around the nest from which the pig(s) took stems was delimited in the field with rope, using the stumps farthest from the nest as the outer boundary. Within the ''affected area'' all free-standing woody plants ≥70 cm tall and <2.0 cm dbh not taken by pigs were tagged, mapped, identified, and measured for BD, height, and dbh (where applicable). Diameters for trees between 1 and 2 cm dbh were available from the most recent census of the 50-ha plot. However, we also measured many of these trees in the field and used our measurements preferentially over those available from the 50-ha plot data set when possible. In each nest, all plants that had been uprooted entirely were measured and counted.

The total number of stems damaged, including those killed, within the affected area during the construction of one of the 10 nests investigated in detail includes the number of stumps plus the number of uprooted individuals found in the nest. The proportion of stems damaged for each nest within the affected area represents the total number of stems damaged divided by the total number of stems damaged and undamaged.

We investigated all plants ≥70 cm tall and <2.0 cm dbh utilized by pigs. Pigs often uproot plants smaller than this, but the impact on the overall understory structure decreases with the size of plants used. In addition, the largest pigs occasionally use woody plants ≥2.0 cm dbh, but usage of such large plants was rare, with <0.5% of plants used to construct the 10 pig nests examined in detail ≥2.0 cm dbh. Consequently, plants above this size threshold were not included in this study. To quantify the sizes of plants damaged by pigs to construct nests, plants were divided into three size classes: (1) ≥70 cm tall and <0.5 cm dbh, (2) 0.5–0.99 cm dbh, and (3) 1.0–2.0 cm dbh.

Data analysis

It is important to note that analyses based on the 10 detailed nests and their affected areas included all free-standing woody plants. There are a number of woody climbers at PFR that may not begin climbing until they are 2.0 cm dbh. Consequently, some lianas were included in the data set, even in the largest size class. Approximately 17% of free-standing plants in affected areas around pig nests that were not damaged by pigs were lianas. Results of all analyses based on the 50-ha plot tags found in pig nests or around adjacent stumps apply only to trees ≥1.0 cm dbh because the 50-ha plot data set does not include lianas.

In several analyses we restricted the data to only those nests from the 1996 survey. This should allow for the most precise data on trees available to pigs at the time of construction, because all but two of the nests from the 1996 survey were constructed after the 50-ha plot recensus workers moved through a given area. As a result, all new recruits into the 50-ha plot, i.e., trees ≥1.0 cm dbh, had been tagged and all plot trees were measured with mortality or survival determined recently.

dbh–BD regressions

To estimate dbh from BD (basal diameter), we used generalized additive models (GAM; Hastie and Tibshirani 1990) to fit logistic regression models allowing a smooth relationship between BD and the probabilities of falling into each of the three size classes (Venables and Ripley 1997). We used a data set of 7000 saplings with known BD, dbh, and height from this and another study from Pasoh (Ickes et al. 2001). Models were fit using stems of BD $<$ 5.0 cm. Many saplings at PFR have been snapped at some time in the past by pigs, but subsequently have resprouted. As a result, it is not uncommon for a sapling to have a relatively large BD for its height because the new shoot has not yet attained the pre-damage height. In these cases, the point of stem snap is obvious because the stem does not taper smoothly with increasing height, but rather decreases abruptly in size. Consequently, separate models for previously damaged ($n = 1791$) vs. undamaged ($n = 5130$) saplings were fit for each of the four size classes.

We expected that liana and tree saplings would have different BD–dbh relationships, but separate models for lianas and trees were not used for three reasons: (1) separate models gave quite similar fits; (2) it was not always possible to distinguish between trees and lianas, particularly for stumps that did not resprout; and (3) there were not enough lianas in each size class to fit the models.

TABLE 1. Number of woody stems (mean ± SD) that were snapped, uprooted, or undamaged within the affected areas of 10 pig nests at Pasoh Forest Reserve, Peninsular Malaysia.

Size class	No. snapped	No. uprooted	Total damaged	No. undamaged saplings	Stems damaged (%)
Saplings <0.5 cm dbh, >70 cm tall	88.0 ± 45.4	113.4 ± 58.5	201.4 ± 80.6	142 ± 72.9	58.9 ± 15.0
Saplings 0.5–1.0 cm dbh	32.9 ± 13.8	7.3 ± 4.3	40.2 ± 16.5	36.2 ± 23.0	53.6 ± 13.3
Saplings 1.0–2.0 cm dbh	24.4 ± 16.7	0.9 ± 1.1	25.3 ± 17.4	67.6 ± 30.9	25.4 ± 14.9
All plants	145.3 ± 49.1	121.6 ± 59.9	266.9 ± 85.7	245.8 ± 115.1	53.0 ± 9.9

Distances of stumps to nests and between nests

Only nests located >20 m from the boundary of the 50-ha plot were used to calculate the distances to trees used in nest construction and the distances between nests. The coordinates of the nest were determined during the three pig nest surveys, and the coordinates for the stumps with tags and the tags found in the nests came from the 50-ha plot data set.

We assessed whether the spatial distribution of pig nests was random by comparing the number of nests within distance d of a nest to the expected number for a Poisson process (Venables and Ripley 1997). This was done for three data sets of nests: (1) new- and medium-aged nests from the 1996 pig nest survey (16 ha), (2) new- and medium-aged nests from the 1998 pig nest survey (20 ha), and (3) all nests from the three surveys within the plot boundaries (16 ha). That areas used in analyses are <25 ha and vary among years reflects the fact that some subplots were missed during pig nest surveys. The areas used in the spatial analyses are the largest contiguous set of subplots that were searched for pig nests.

We also asked whether pigs chose nest locations based on local stem density. Stem density within a 10 m radius of nests from the 1996 nest survey (n = 136 nests) was compared to stem density within a 10 m radius of 1000 randomly selected points ≥10 m from the boundary of the 50-ha plot.

Tree species used as construction material

We tested whether pigs used saplings of all species in proportion to their abundance in the area surrounding the nest site, using only the 1996 pig nest survey. All trees with dbh 1–2 cm from the tree plot based on the 1995 50-ha plot survey found within a 15 m radius of each nest from the 1996 pig nest survey were used in analyses. Whether the proportion of individuals taken was the same across species was examined using a likelihood ratio test for homogeneity of proportions within a contingency table (Fienberg 1980). The same analysis was conducted at the family level by including all individuals of species belonging to the family.

We tested whether a small number of families of interest were taken at rates significantly different than the overall proportion of individuals. The analyses consisted of a simple test for equality of proportions with binomial data. We predicted that the Ebenaceae would be taken less often because the dense wood would be difficult for pigs to bite through, and the Anacardiaceae would be taken less often because many species in this family have noxious black resin. We did not have specific predictions with regard to the Euphorbiaceae and Dipterocarpaceae, but tested them because they are the dominant plant families.

Annual mortality of trees 1–2 cm dbh at PFR

The differential equations of Paciorek et al. (2000) were used to estimate annual mortality and annual mortality plus resprouting rates of trees 1–2 cm dbh in the 25-ha study area. Equations were based on data from the 50-ha plot tree surveys in 1990 and 1995.

To estimate the number of 50-ha plot trees of 1–2 cm dbh taken by pigs on a per nest basis, we used the nest data from 1996 for nests ≥10 m from the plot edge to avoid undercounting the number of individuals taken. All 50-ha plot tags for trees 1–2 cm in dbh found in the nests and those from adjacent stumps were counted. Damaged trees were included only if the main stem had been snapped.

The total number of 1–2 cm dbh trees in the 50-ha plot killed from pig nest construction in a year was estimated by calculating:

$$(\text{no. tags/nest} \times \%\ \text{survival}) \times \text{no. nests/yr.}$$

Percentage survival is the percentage of stems 1–2 cm in dbh that were damaged by pigs during nest construction and that survived to 36 months after damage occurred (Ickes et al. 2003). This number was then compared with the total number estimated to die in a year from all causes based on the 1990 and 1995 Pasoh surveys.

RESULTS

Composition of individual nests

Overall, 643 pig nests were enumerated within the 25-ha study area: 302 in 1995, 148 in 1996, and 193 in 1998. From these nests, 3480 tags from trees >1.0 cm dbh were recovered. Nest size, and consequently the area impacted, varied considerably among nests: for the 10 nests, the area affected was 244 ± 112 m^2 (mean ± SD), with a range of 93–456 m^2. There was also considerable variation among the sizes of plants utilized in nest construction (Table 1). The percentage of plants ≥70 cm tall and <0.5 cm dbh damaged in the affected area of a nest ranged from 28% to 78%, whereas the extent of damage for plants 1–2 cm dbh

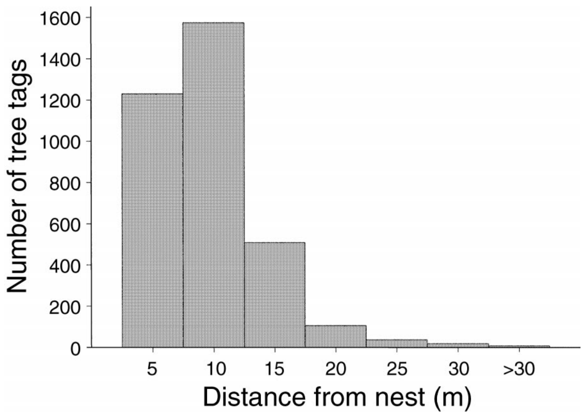

FIG. 1. The distance from pig nests to the locations of the 3480 trees ≥1.0 cm dbh used in nest construction. Tree coordinates come from the 50-ha data set, and nest coordinates were mapped during surveys in 1995, 1996, and 1998. Distances for trees with tags found in nests were calculated as a straight line from the nest to the position of the tree. When two or more nests of similar age were close together, stumps were assumed to have been used in the construction of the nearest pig nest.

was 0–47%. When plants from all three size classes were considered together, on average, 53% of all free-standing woody plants ≥70 cm tall and <2.0 cm dbh in the affected area were damaged by pigs. Of the total number of damaged plants, 45% were uprooted and killed, whereas 55% had the main stem snapped. Predictably, however, the percentage of plants uprooted and therefore killed outright was greater for plants of smaller stature: 54% of plants were uprooted in the smallest size category, whereas only 4% of stems were uprooted in the largest class (Table 1).

Number of nests constructed per year

In the 1996 survey of the 25-ha area, 5.6 nests·ha^{-1}·yr^{-1} were constructed, and 4.3 nests·ha^{-1}·yr^{-1} were constructed in 1998. It is unknown how many nests were constructed and subsequently decayed prior to enumeration in each survey period. A number of new and medium-aged nests from 1995 had disappeared within a year, suggesting that the observed 5.6 nests·ha^{-1}·yr^{-1} is indeed an underestimate. For the 1996–1998 survey interval, nest decay occurring during the 24-mo interval means that that the observed 4.3 nests·ha^{-1}·yr^{-1} is a very conservative estimate for the period from 1996 to 1998. Therefore, to account for decayed nests as well as those missed in the survey, we used 6.0 nests·ha^{-1}·yr^{-1} as the best estimate of the number of nests constructed between 1995 and 1996 in the equations for estimating mortality of trees due to pigs.

Distances of stumps to nests and between nests

Pigs gathered woody stems from relatively close to the nest site. More than 80% of trees >1 cm dbh were obtained within 10 m of the nest, and 95% were obtained within 15 m (Fig. 1).

Pigs avoided constructing nests adjacent to the three major trails within the 25-ha study area, particularly where the two largest trails intersect. Also, the extreme northeastern portion of the study area represents the only non-flat area surveyed, and pigs may have built less frequently on the slopes. Aside from areas near the trails and possibly slopes, nests were observed throughout the study area.

Nests from 1996 were clumped at distances of 30–170 m (Fig. 2A), whereas nests from 1998 were clumped at distances >40 m (Fig. 2B). This suggests that nest-building activity in a given year is concentrated in certain areas within the plot, although it appears to be random at small scales. Most nests were within 30 m of the nearest nest within a survey period, but rarely within 10 m (Fig. 3).

Pigs did not choose nest site locations with stem densities different from the plot. Based on 1000 locations, the density of stems 1–2 cm dbh was 77.0 ±

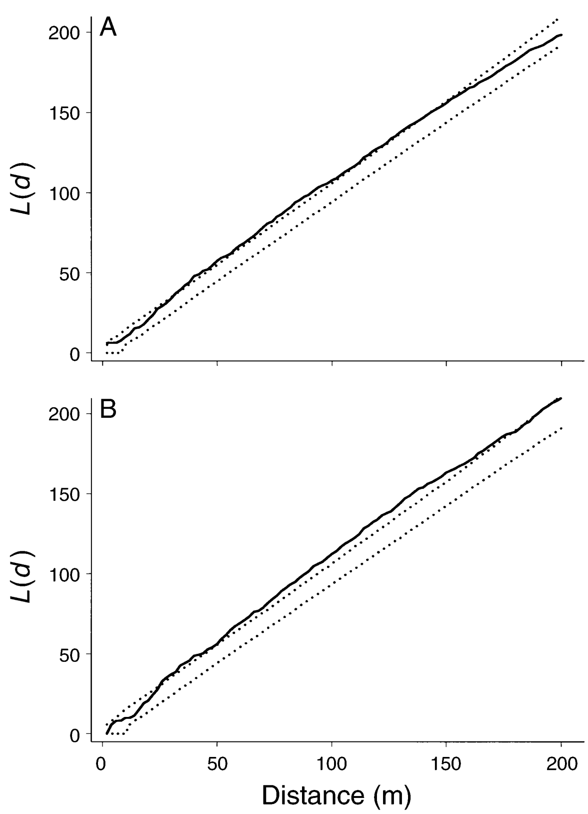

FIG. 2. Analysis of clumping of pig nests from the (A) 1996 and (B) 1998 surveys. The figure shows confidence intervals (dotted lines) that are simulated based on assuming a Poisson process, but fixing the number of points at the actual number of nests observed. $L(d) = \sqrt{K(d)/\pi}$ where $K(d)$ is Ripley's K function. For a Poisson process, $L(d)$ is linear in d, such that values of d for which $L(d)$ is above the confidence bands indicate significant clumping at $P < 0.05$ at that distance scale.

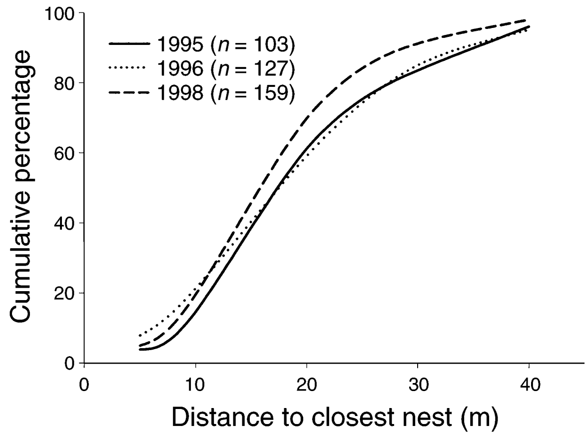

FIG. 3. The percentage of pig nests within *x* meters of the nearest nest within the same survey period. Sample sizes of nests are given parenthetically for each year. Only pig nests of ''new'' and ''medium'' ages were considered for 1995, but all nests were used for 1996 and 1998.

1.75 stems (mean ± 2 SE) per 10 m radius circle. The mean for the 1996 nest locations was 74.9 ± 4.7 stems (mean ± 2 SE).

Annual mortality of trees 1–2 cm dbh at PFR

Overall annual mortality of trees 1–2 cm dbh from all causes (pig and non-pig) was estimated to be 1.84% and the annual percentage of trees suffering stem snap damage or death was 3.52%. The 816 tags from the 134 pig nests in 1996 gave an estimate of 6.1 trees 1–2 cm dbh per nest. Using our estimate of 6.0 nests·ha^{-1}·yr^{-1}, 36.5 individuals were killed or damaged per year because of pig nest construction. We assumed that 35.6% of damaged individuals die (Ickes et al. 2003), which gave an estimate of 2.1 deaths·nest^{-1}·yr^{-1}, or 13.0 deaths·ha^{-1}·yr^{-1}.

Based on the annual mortality rates computed for trees 1–2 cm dbh and 2471.4 stems/ha of 1–2 cm dbh, there were an estimated 45.5 deaths and 85.5 deaths plus resprouts per hectare in this size class. This suggests that trees killed for pig nest construction comprised 29% (13.0/45.1) of the total mortality due to all causes, and 43% (36.5/85.5) of total mortality and resprouting combined. Annual mortality attributable to pig nest building alone was 0.53% for trees 1–2 cm dbh at Pasoh Forest Reserve.

Tree species used as construction material

For the 1996 survey, 833 or 3.4% of trees 1–2 cm dbh were taken of 24 396 available. There was no evidence for species-level differences in the percentage taken (G^2 = 611, df = 622, P = 0.62), but it is important to note that sample sizes were small for each species due to the extraordinary diversity in this forest.

There were large differences in the percentage of individuals taken at the family level (G^2 = 135, df = 69, P < 0.0001; Fig. 4). Individuals from the Dipterocarpaceae were used in nest construction more frequently (6.5%) than all other trees combined (3.4%; P < 0.0001). The most common dipterocarp species at PFR, *Shorea maxwelliana*, accounted for 40% of all dipterocarps damaged and had 6.6% of stems damaged within affected areas. However, 6.4% of the stems from the other dipterocarp species available were also taken, suggesting that all dipterocarps were chosen preferentially over non-dipterocarp species. As predicted, trees in the Ebenaceae, all in the genus *Diospyros*, were taken less frequently than all trees combined (2.0% vs. 3.4%; P = 0.01), but there were no differences in the percentage taken for the Euphorbiaceae (3.8% vs. 3.4%; P = 0.29) or Anacardiaceae (3.8% vs. 3.4%; P = 0.73).

DISCUSSION

The building of nests by pigs seems to be having a profound impact on the understory vegetation and tree regeneration at Pasoh Forest Reserve. Nests accounted for 28.9% of the overall mortality, and 42.7% of the mortality plus damage in the study area for trees in the 1–2 cm dbh size class. Pigs alone caused 0.53% annual mortality of trees 1–2 cm dbh at PFR. Given that overall mortality for trees of this size class at PFR was 1.8%, this a remarkably high mortality rate attributed to a single causal agent. The only other examples of mam-

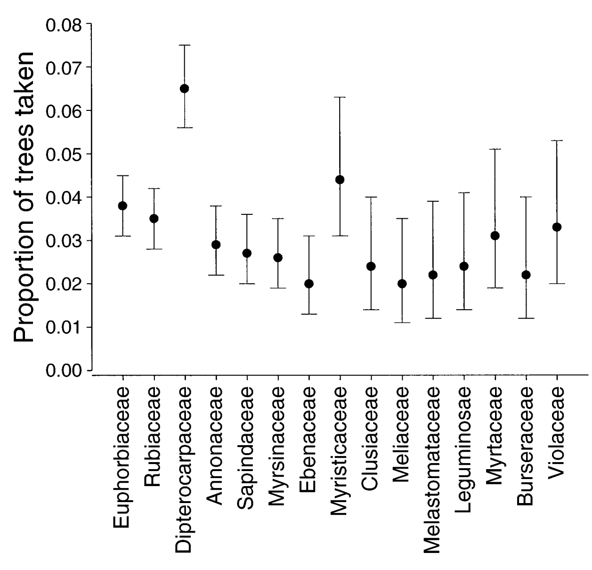

FIG. 4. Proportion of stems, by family, within a 15-m radius of each pig nest that were in used nest construction. All nests from the 1996 survey were used in calculating the proportion taken. Families are arranged from left to right on the *x*-axis in decreasing order of the number of stems from that family available to pigs for nest construction: 2970 saplings 1–2 cm dbh were available from the Euphorbiaceae, whereas 515 were available from the Violaceae. Only families with >500 stems available are shown. Bars represent the 95% confidence interval of the proportion taken, based on the normal approximation to the binomial distribution with continuity correction.

mals that are known to cause comparable tree mortality and damage are beavers, through foraging and dam building and subsequent changes in hydrology in the temperate zone, and locally dense populations of elephants, through foraging and trampling in the tropics (Barnes and Dibble 1988, Naiman et al. 1988, Struhsaker et al. 1996, Struhsaker 1997, Donkor and Fryxell 1999).

Our results suggest that pigs are playing a large role in understory plant dynamics at Pasoh Forest Reserve; however, our data underestimate the damage caused by pigs for several reasons. First, it is unlikely that we encountered all pig nests during the 25-ha surveys. Second, a considerable number of tags from trees damaged or killed by pigs may not have been found. Third, we only measured damage to free-standing woody plants. Pigs clearly prefer to use leaves of understory, broad-leaved monocot species when available (K. Ickes, *personal observations*), particularly from the palm genus *Licuala* and terrestrial gingers and aroids. Unfortunately, there are no demographic background data on these groups of plants at PFR. Broad-leaved understory plants are not currently common at PFR; we speculate that this is due to pigs using them preferentially as nesting material.

Pig nest areas as understory gaps

The average understory area affected by pig nests at PFR was 244 m^2. Within this area, pigs removed or severely damaged >50% of the understory woody vegetation, essentially creating an understory gap (sensu Connell et al. 1997). The area affected per nest was the equivalent of a ''large'' canopy gap, and was larger than 76% of canopy gaps (>20 m^2 in projected area) from Barro Colorado Island in Panama, 95% of canopy gaps at La Selva, Costa Rica (Brokaw 1982, Sanford et al. 1986), and 96% of canopy gaps at PFR (S. C. Thomas, *unpublished data*). Although canopy gaps result in dramatic increases in light and temperature, alter soil nutrient and water conditions, and decrease competition for light and nutrients (Denslow 1987), such changes are comparatively small in the understory gaps of pig nests because only understory plants are damaged. Connell et al. (1997) reported that growth rates are often higher in understory gaps, but this may not be the case for understory gaps at PFR. Ickes et al. (2003) followed pig-created stumps for 36 months after nest construction and found remarkably slow growth rates. In areas of high nest abundance at PFR, virtually all remaining understory plants are either too large to be used by pigs in nest construction (>2.5 cm) or are short stumps with slowly growing resprouts. In a separate study, Ickes et al. (2001) constructed pig exclosures at PFR and found that growth rates were higher inside fences, where pigs had no access, a result attributed to negative effects of soil disturbance in control plots by pig rooting. This suggests that the detrimental effects on plant growth by soil disturbance via pig rooting may counterbalance some of the expected advantages to saplings undamaged during nest construction.

Estimates for conversion of forest to canopy gaps range from 0.7% to 1.2% per year (Denslow 1987). The 6.0 pig nests$\cdot ha^{-1} \cdot yr^{-1}$ created at PFR affected 1366 m^2, or 1.4% of the area. As a result, pig nest building is impacting annually an understory area at least as large as that affected by canopy gap formation. We documented the impacts of nest building on the plants damaged in the construction process. The resulting decrease in understory biomass is likely to affect other organisms and ecological processes, but such secondary effects remain to be investigated.

Extensive understory damage by pigs: a recent phenomenon

In the absence of a detailed historical record of pig density at PFR or any other Asian tropical forest, it is impossible to state conclusively that the large number of pigs and pig nests at PFR is a relatively new phenomenon. However, pig densities at PFR equaled 47 and 27 individuals/km^2 in 1996 and 1998, respectively, which is 10–100 times higher than estimates of *Sus scrofa* density in other mainland forest habitats in its native range (Ickes 2001). Indeed, the only other estimate of pig density in Malaysia, from a lowland dipterocarp forest in northern Peninsular Malaysia, was <1.0 individuals/km^2 (Diong 1973). Ickes (2001) and Ickes and Williamson (2000) hypothesized that *S. scrofa* thrive at PFR due to the disappearance of predators from PFR and presence of an abundant, year-round food supply from the fruit of African oil palms (*Elaeis guineensis* Jacq.), which are found in plantations surrounding the reserve. The last confirmed tiger sighting at PFR was in the 1960s, while surrounding forest began to be to converted to African oil palm plantations in the 1970s and 1980s. These lines of evidence suggest that the number of pigs at PFR and, subsequently, pig nests, have increased dramatically in the past 30 years.

Changes in forest composition at PFR

Dipterocarp species were damaged by pigs about twice as frequently as species from other families. Nest building by *Sus scrofa* may affect the species composition at PFR through their preference for saplings from the Dipterocarpaceae and through the high mortality rates of dipterocarps following pig damage compared to other trees at PFR (Ickes et al. 2003). Thirty-six months after stumps were created naturally (by pigs) or experimentally, dipterocarps had the lowest survivorship of 19 plant families examined in the same forest (Ickes et al. 2003). Dipterocarps comprised 24% of aboveground plant biomass at PFR in 1990 (Kochummen et al. 1990). If pig density and the number of nests constructed annually at PFR remain at levels measured between 1996 and 1998, there may be a shift away from dominance by the Dipterocarpaceae in favor of other species. Results of the present study suggest that nest-building behavior of *Sus scrofa* may have large impacts on tree demography, and, in the long term, tree community composition.

Acknowledgments

We thank Kate Walker, Brian Funk, Scott Ickes, Rob Tizard, and Alison Styring for assistance in the field. Saara DeWalt and two anonymous reviewers made helpful suggestions that improved this manuscript. K. Ickes received funding from a Board of Regent's Fellowship from Louisiana State University, the Center for Tropical Forest Science, and a Grants-in-Aid of Research from the National Academy of Sciences through Sigma Xi. C. J. Paciorek acknowledges support from the National Science Foundation under a VIGRE grant to the Department of Statistics, Carnegie Mellon University. S. C. Thomas was funded by the National Science Foundation. We are grateful to Dr. Abdul Razak, Director General of the Forestry Research Institute Malaysia (FRIM), for permission to conduct research at Pasoh Forest Reserve. The 50-ha tree plot at Pasoh is part of the Center for Tropical Forest Science, a global network of large-scale demographic tree plots. The Pasoh 50-ha plot has been generously funded by FRIM and the National Science Foundation, USA.

Literature Cited

Barnes, W. J., and E. Dibble. 1988. The effects of beaver in riverbank forest succession. Canadian Journal of Botany **66**:40–44.

Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica **14**:158–160.

Connell, J. H., M. D. Lowman, and I. R. Noble. 1997. Subcanopy gaps in temperate and tropical forests. Australian Journal of Ecology **22**:163–168.

Curran, L. M., I. Caniago, G. D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C. E. Nirarita, and H. Haeruman. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. Science **286**:2184–2188.

Curran, L. M., and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. Ecological Monographs **70**:101–128.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics **18**:431–451.

Diong, C. H. 1973. Studies of the Malayan wild pig in Perak and Johor. Malay Nature Journal **26**:120–151.

Donkor, N. T., and J. M. Fryxell. 1999. Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. Forest Ecology and Management **118**:83–92.

Fienberg, S. E. 1980. The analysis of cross-classified categorical data. MIT Press, Cambridge, Massachusetts, USA.

Hastie, T., and R. Tibshirani. 1990. Generalized additive models. Chapman and Hall, New York, New York, USA.

Ickes, K. 2001. Hyper-abundance of native wild pigs (*Sus scrofa*) in a lowland Dipterocarp rain forest of Peninsular Malaysia. Biotropica **33**:682–690.

Ickes, K., S. J. DeWalt, and S. Appanah. 2001. Effects of native pigs (*Sus scrofa*) on the understory vegetation in a Malaysian lowland rain forest: an exclosure study. Journal of Tropical Ecology **17**:191–206.

Ickes, K., S. J. DeWalt, and S. C. Thomas. 2003. Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. Journal of Ecology **91**:222–233.

Ickes, K., and G. B. Williamson. 2000. Edge effects and ecological processes—are they on the same scale? Trends in Ecology and Evolution **15**:373.

Jachmann, H., and T. Croes. 1991. Effects of browsing by elephants on the *Combretum*/*Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. Biological Conservation **75**:13–24.

Jensen, P. 1989. Nest site choice and nest building of free-ranging domestic pigs due to farrow. Applied Animal Behaviour Science **22**:13–21.

Kochummen, K. M., J. V. LaFrankie, and N. Manokaran. 1990. Floristic composition of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. Journal of Tropical Forest Science **3**:1–13.

Medway, L. 1963. Pigs' nests. Malay Nature Journal **17**:41–45.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience **38**:753–762.

Okuda, T., M. Suzuki, N. Adachi, K. Yoshida, K. Niiyama, N. S. M. Noor, N. A. Hussein, N. Manokaran, and M. Hashim. 2003. Logging history and its impact on forest structure and species composition in the Pasoh Forest Reserve: implications for the sustainable management of natural resources and landscapes. Pages 15–34 *in* T. Okuda, N. Manokaran, J. Matsumoto, K. Niiyama, S. C. Thomas, and P. S. Ashton, editors. Pasoh: ecology of a lowland rain forest in Southeast Asia. Springer-Verlag, Tokyo, Japan.

Oliver, W. L. R., editor. 1993. Pigs, peccaries, and hippos. IUCN [International Union for the Conservation of Nature], Gland, Switzerland.

Paciorek, C. J., R. Condit, S. P. Hubbell, and R. B. Foster. 2000. The demographics of resprouting in tree and shrub species of a moist tropical forest. Journal of Ecology **88**:765–777.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs **45**:285–305.

Sanford, R. I.,Jr., H. E. Braker, and G. S. Hartshorn. 1986. Canopy openings in a primary neotropical lowland forest. Journal of Tropical Ecology **2**:277–282.

Shachak, M., S. Brand, and Y. Gutterman. 1991. Porcupine disturbance and vegetation pattern along a resource gradient in a desert. Oecologia **88**:141–147.

Struhsaker, T. T. 1997. Ecology of an African rain forest. University of Florida Press, Gainesville, Florida, USA.

Struhsaker, T. T., J. S. Lwanga, and J. M. Kasenene. 1996. Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. Journal of Tropical Ecology **12**:45–64.

Tardiff, S. E., and J. A. Stanford. 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology **79**:2219–2228.

Venables, W. N., and B. D. Ripley. 1997. Modern applied statistics with S-Plus. Springer-Verlag, New York, New York, USA.