

Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest

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ABSTRACT. Large mammals often play important roles in determining the structure and composition of plant communities. This study focused on the extent to which wild pigs (*Sus scrofa*) influence the dynamics of tree seedlings and saplings in a lowland rain forest at Pasoh Forest Reserve in West Malaysia. Native wild pigs are common in the study area and may significantly influence growth and survivorship of woody plants in the understorey through several activities – namely, nest building, soil rooting and seed predation. To test experimentally the impact of pigs on the plant community, eight 49-m² exclosures were constructed. After 2 y, the number of recruits inside exclosures was three times greater than in unfenced control plots. Stem density was highly correlated with species richness, which also increased significantly inside exclosures. Height growth of plants was greater in the exclosures by 52.5% for trees between 1 and 7 m tall. Trees less than 1 m tall, however, exhibited no differences in growth. Mortality of plants also did not differ between treatments. The observed differences between exclosure and control plots can be attributed to soil-rooting and seed predation, suggesting that these two behaviours of wild pigs are important to plant dynamics in the understorey.

KEY WORDS: exclosure, Malaysia, mortality, plant–animal interactions, seed predation, soil disturbance, *Sus scrofa*

INTRODUCTION

The influential role of vertebrate species in structuring plant communities is increasingly well documented. Medium to large bodied mammals can alter

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dynamics of plant species at population (Augustine & Frelich 1998, Bergelson & Crawley 1992) or community levels (McInnes *et al.* 1992, Schreiner *et al.* 1996), alter vegetation structure (McNaughton & Sabuni 1988) and species composition (Anderson & Loucks 1979), retard forest regeneration (Struhsaker *et al.* 1996), and decrease (Agnew *et al.* 1986, Virtanen *et al.* 1997) or increase richness (Guterman 1998). Significant effects on plant dynamics have resulted from grazing by lemmings (Virtanen *et al.* 1997), prairie dogs (Archer *et al.* 1987) and reindeer (Wegener & Odasz-Albrigtsen 1998); browsing by moose (Pastor *et al.* 1988) and elephants (Barnes *et al.* 1994); burrowing by pocket gophers (Huntly & Inouye 1988); dam building by beavers (Naiman *et al.* 1988); digging for subterranean food by grizzly bears (Tardiff & Stanford 1998), porcupines (Guterman 1982) and badgers (Platt 1975); seed predation by various species (Blate *et al.* 1998, De Steven & Putz 1984, Schupp 1988, Terborgh *et al.* 1993, Terborgh & Wright 1994); or trampling and mechanical damage (Plumpton 1993). The common or wild pig (*Sus scrofa*) exhibits several behaviours that may have large influences on understorey vegetation: soil rooting, nest building and seed predation. Here we examine the extent to which this species alters plant communities, in this case, the woody sapling community in a lowland rain forest in Malaysia.

Sus scrofa has a natural geographical range that extends throughout Europe and Asia as far south and east as the Malay Peninsula and the islands of Sumatra and Java. The species occupies a diversity of habitat and vegetation types. *Sus scrofa* has also been introduced in numerous locations outside their native ranges and feral populations are well established in New Zealand (Caughley 1970), Australia (Hone 1990), North America (Singer 1981), Hawaii (Stone & Loope 1987), the Galapagos (Coblentz & Baber 1987) and numerous other islands (Baber & Coblentz 1986, Baron 1982, Challies 1975). Although *S. scrofa* is known to have detrimental effects on forest communities where introduced, little is known about its impact on communities to which they are native.

Sus scrofa is an omnivorous species, so diets vary greatly among habitats and geographic locations (Diong 1973, Henry & Conley 1972, Klau 1992). In all areas, however, large proportions of their diets are subterranean in origin and the animals regularly root through soil (Genov 1981, Singer 1981). Rooting may adversely affect vegetation directly by displacing and killing seedlings or indirectly by altering physical properties of the soil, changing nutrient dynamics (Lacki & Lancia 1983, Singer *et al.* 1984), or facilitating the spread of exotic vegetation (Aplet *et al.* 1991). Conversely, rooting may be beneficial to plants: in the only study to investigate the effects of rooting on plant growth, pig rooting increased shoot elongation of large beech trees in North America, a result attributed to increased humus breakdown and greater aeration of soils (Lacki & Lancia 1983).

A second aspect of pig behaviour that may alter the plant community is frugivory and subsequent seed mortality. Throughout their range, pigs are known to eat large quantities of fruits and seeds when available. In the Sunda Shelf region of Southeast Asia, mast fruiting occurs on a supra-annual scale for many plant species (Whitmore 1984). One hypothesis for fruiting synchrony is predator satiation during fruiting events (Kelly 1994). Wild (*S. scrofa*) and bearded pigs (*S. barbatus*) are thought to be two of the most important predators of fallen fruits and seeds and may in large part account for the mast fruiting phenomenon in Southeast Asia (Curran & Leighton 2000, Curran & Webb 2000).

Nest building is yet another behaviour of pigs that may influence plant dynamics. Prior to giving birth, female pigs harvest vegetation to build a mound under which they deliver their young. In primary lowland rain forest of Peninsular Malaysia, pigs form nests primarily from woody tree saplings 40–350 cm in length that they uproot or snap off. As a single nest may comprise over 500 stems, nest building may reduce stem density and increase plant mortality dramatically at a local scale.

We quantified the impact that *S. scrofa* has on understorey woody plant density and diversity in lowland rain forest at Pasoh Forest Reserve (PFR) in Peninsular Malaysia. When this study was initiated, we suspected that pig densities in PFR were elevated from historical or natural levels, due to an absence of natural predators of pigs in the reserve and an abundant food source in agricultural plantations surrounding the reserve (see Methods). We expected that this unusually high density of pigs was having strong, negative effects on understorey saplings. Subsequently, line transect studies have shown that density of *Sus scrofa* is indeed many times higher at PFR than other mainland forests in Europe and Asia (Ickes & Williamson 2000).

In experimental plots we removed the possible influences on plants of pig rooting, nest building and frugivory. We predicted that excluding pigs would decrease sapling mortality and increase woody plant recruitment, stem density and species richness. Because we investigated the effects of rooting on understorey saplings, we hypothesized a priori that rooting would have negative effects on plant growth, particularly on plants less than 100 cm tall, because of their smaller size and less expansive root systems. Finally, we expected that changes in the composition of plant life forms would occur as a result of pig activity. If pigs knock over and kill small plants when rooting, the probability of an individual surviving should increase with size; taller plants should have more extensive root systems and hence have more anchor support (Bratton 1975). Therefore, potentially fast growing plants, such as lianas, might survive rooting activity better, consequently altering the liana to tree proportions. We thus expected that the proportion of woody stems comprising lianas would be higher outside exclosures.

METHODS

Study system

Pasoh Forest Reserve lies 110 km southeast of Kuala Lumpur in the state of Negeri Sembilan, Peninsular Malaysia (2°59'N, 102°18'E). The reserve comprises a core area of 650 ha of primary lowland dipterocarp forest and a 650 ha buffer zone of selectively logged lowland forest regenerating from logging that occurred 40 y ago. Another 650–1000 ha of primary hill dipterocarp forest comprises the eastern portion of the reserve. Aside from a corridor of hill forest that connects PFR to the southern end of the main mountain range, the remaining perimeter (c. 85%) is bordered by mature African oil palm (*Elaeis guineensis* Jacq.) plantations. The flora of PFR is exceptionally diverse, with over 800 tree species ≥ 1.0 cm dbh (diameter at breast height) recorded in a 50-ha tree plot (Kochummen 1997). Annual rainfall is c. 2000 mm with a known range of 1700–3200 (Kochummen *et al.* 1990). Monthly rainfall means exceed 100 mm, providing an aseasonal climate.

Exclosure design

Exclosures were constructed between 30 June and 11 July 1996 in primary forest south of the permanent, 50-ha study plot. Beginning at the origin of this plot, an exclosure was constructed 40 m to the south, and at subsequent 40-m intervals eastward. Exclosures consisted of a 7-m \times 7-m \times 1.5-m chain-link fence with 4-cm² mesh. To ensure that pigs did not root under the fence, up to four rows of barbed wire encircled each fence, from ground level to 60 cm in height. Exclosures were open above. Because of this open-top design and the wide mesh size, it did not appear that the exclosures altered light, wind speed, rainfall or other microclimate conditions.

Two control plots were paired with each exclosure in a randomized block design. These were placed 1 m outside of the exclosures on two of the four sides. Control plots were placed on the two sides that subjectively most closely resembled the vegetation structure within the paired experimental plot. A 5-m \times 5-m plot was centred within each exclosure and each control area.

Exclusion of vertebrates

Due to the wide mesh size of the fence and open top design, we assumed that all birds, rodents, civets (several of which are partially frugivorous) and primates could readily enter the exclosures. Consequently, the only potential vertebrate seed predators or herbivores excluded were large terrestrial mammals. Lowland rain forests in Peninsular Malaysia historically contained a number of medium to very large terrestrial herbivores. Indian elephant (*Elephas maximus*), Malayan tapir (*Tapirus indicus*), Javan rhinoceros (*Rhinoceros sondaicus*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), barking deer (*Muntiacus muntjak*), greater mouse-deer (*Tragulus napu*), lesser mouse-deer (*T. javanicus*), Malayan porcupine (*Hystrix*

brachyura), brush-tailed porcupine (*Atherurus macrourus*), wild pig (*Sus scrofa*) and bearded pig (*S. barbatus*) all probably occurred at PFR until the twentieth century and some until quite recently (Medway 1983). Currently, however, most of these species are extinct or rare within PFR because of the small reserve size, relatively homogeneous habitat within the remaining area, poaching, habitat fragmentation in the surrounding area, relative isolation and removal of potentially dangerous animals from the surrounding oil palm tree plantations by the Wildlife Department. Therefore, the only herbivores excluded during this study were the focal organism *S. scrofa*, both porcupine species, and the lesser mouse-deer. Both porcupines are still present at Pasoh but at apparently low densities; only one individual porcupine was seen during > 250 h walking line transects at dusk and dawn, compared with hundreds of wild pigs (K. Ickes, unpubl. data). Lesser mouse-deer, though common at Pasoh, neither build nests for reproduction nor disturb soil by digging. They are granivorous, however, and therefore excluding this species may confound the interpretation of results with regard to seed predation by pigs vs. mouse-deer.

Vegetation sampling

For the initial survey, plants were measured between 12 August and 21 September 1996. Within experimental ($n = 8$) and control ($n = 16$) plots, all woody, free-standing plants ≥ 30 cm height were identified, mapped and measured for basal diameter, dbh (if applicable), and height up to 740 cm using a telescoping measuring pole. Free-standing lianas were included in the survey. Plants were tagged within the exclosures. Because pigs are known to chew aluminium tags, plants in the controls were carefully mapped but not tagged.

The second survey took place from 1–20 August 1998. We recorded the same measurements or noted mortality, and all new plants that had recruited into the ≥ 30 cm height category were added (hereafter called recruits). Additionally, in 1998 only, all seedlings of woody plants < 30 cm tall were counted but not identified in 1-m \times 1-m plots in the corners of the 5-m \times 5-m study plots (hereafter called seedlings).

Plant species were identified by K. Ickes, primarily based on prior identification of species for the 50-ha permanent plot at Pasoh. Unknown species were collected and identified at the herbarium of the Forestry Research Institute of Malaysia with assistance from herbarium staff and visiting specialists.

Mast-fruiting at PFR

Mast-fruiting occurred in 1983, 1990 and 1996 at PFR, although very little fruit fell before completion of the fences on 11 July 1996. Prior to completion of the vegetation sampling on 21 September 1996, however, most fruits had fallen and many had begun to germinate, creating a dense seedling carpet in some areas. None of the new seedlings from the mast event were included in 1996, however, because they were not tall enough (≥ 30 cm) at the time of the survey.

Data analysis

Statistical analyses were conducted using SAS version 6.12. Data with non-normally distributed residuals were log-transformed. Several variables did show deviations from normality, even after transformations. While ANOVA is a robust analysis and can tolerate even substantial deviations from normality, P-values should be judged accordingly. Using PROC MIXED, we tested the effect of treatment (exclosure vs. control) on recruitment, mortality, growth, seedling number, overall stem density, stem density within different size classes, proportion of stems 30–100 cm tall made up of lianas, species richness and Fisher's log series α . Treatment was a fixed effect and block ($n = 8$) was a random effect in all ANOVAs. For variables measured in both years the 1996 values were used as covariates. In addition, for recruitment and mortality the number of stems in 1996 was used as a covariate. For growth, the height of trees in 1996 was used as a covariate. The number of individuals in the four seedling subplots established in 1998 were combined for plot comparisons.

Growth was determined as the difference in height between 1998 and 1996. Growth was compared for trees initially between 1–7 m tall, for trees initially between 30–100 cm tall, and for lianas initially between 30–100 cm in height. In addition, we tested species-specific growth responses to pig exclusion in the eight species that had more than 50 stems survive from 1996 to 1998.

Changes in diversity were examined in two ways: number of species and Fisher's log series α index. For Fisher's α , values of the x-parameter were calculated in SAS using a simple iterative program. Only individuals with species level identifications or morphotypes were included in the diversity analyses, resulting in 139 stems (5.7% of total) deleted from the 1996 calculations and 132 stems (4.6% of total) from the 1998 calculations. Species richness values are thus underestimated because many of the unidentified individuals represent rare species.

Survival as a function of height in the control vs. exclosure plots was analysed by logistic regression with a binomial distribution and the logit link function (PROC GENMOD).

RESULTS

The 1996 survey of free-standing stems ≥ 30 cm tall consisted of 2452 individuals and 278 species (including 33 morphospecies). Species and family dominance were low in the study area – the most common species *Xerospermum norhanianum* accounted for only 4.3% of the total number of stems and only 5.2% of stems between 30 and 50 cm tall (Table 1). Lianas composed 490 (26%) of the 1962 stems between 30 and 200 cm tall. Between 1996 and 1998, 229 plants died and 629 stems recruited into the ≥ 30 cm size class. Species dominance was much higher among recruits than among plants from the 1996 survey, with the most abundant species comprising 21.8% and the three most abundant accounting for 53.3% of all recruits (Table 1).

Table 1. Ten most common species from the initial survey in 1996 and eight most common species that recruited into the ≥ 30 -cm size class between 1996 and 1998, Pasoh Forest Reserve, Malaysia. Number of stems includes individuals from all size classes, whereas number of small stems includes only plants between 30 and 50 cm tall. In the Habit column a 'T' indicates that the species is a tree and 'L' is for liana. *Caesalpinia*, the three dipterocarp species and *Alchornea* all had tremendous fruit crops during the most fruiting of 1996; *Rinorea horneri* probably fruited continuously; and *Willughbeia* had a large fruit crop immediately prior to the 1998 survey. We have no information about the phenology of Morphotype 1 from the Connaraceae.

| Species | Family | Habit | Number of stems | Cumulative % of total stems | Number of small stems | Cumulative % of small stems |
|--|------------------|-------|-----------------|-----------------------------|-----------------------|-----------------------------|
| 1996 survey | | | | | | |
| <i>Xerospermum norhonianum</i> Bl. | Sapindaceae | T | 105 | 4.3 | 53 | 5.2 |
| <i>Anaxigorea javanica</i> Bl. | Annonaceae | T | 82 | 7.6 | 46 | 9.8 |
| <i>Shorea maxwelliana</i> King | Dipterocarpaceae | T | 80 | 10.9 | 29 | 12.7 |
| <i>Caesalpinia parviflora</i> Prain ex King | Leguminosae | L | 68 | 13.7 | 51 | 17.7 |
| <i>Ardisia crassa</i> C.B. Clarke | Myrsinaceae | T | 63 | 16.2 | 26 | 20.3 |
| <i>Rohmania macrophylla</i> (Hk. F.) Bremek. | Rubiaceae | T | 63 | 18.8 | 28 | 23.0 |
| Morphotype 1 | Connaraceae | L | 55 | 21.0 | 31 | 10.8 |
| <i>Rinorea horneri</i> (Korth.) O.K. | Violaceae | T | 55 | 23.3 | 27 | 28.8 |
| <i>Shorea macroptera</i> Dyer | Dipterocarpaceae | T | 37 | 24.8 | 9 | 29.7 |
| <i>Leptonychia glabra</i> Turcz. | Sterculiaceae | T | 35 | 26.2 | 9 | 30.6 |
| 1998 recruits | | | | | | |
| <i>Caesalpinia parviflora</i> Prain ex King | Leguminosae | L | 137 | 21.8 | | |
| <i>Shorea leprosula</i> Miq. | Dipterocarpaceae | T | 126 | 41.8 | | |
| <i>Shorea macroptera</i> Dyer | Dipterocarpaceae | T | 72 | 53.3 | | |
| <i>Willughbeia coriacea</i> Wall. | Apocynaceae | L | 27 | 57.6 | | |
| <i>Rinorea horneri</i> (Korth.) O.K. | Violaceae | T | 18 | 60.4 | | |
| <i>Dipterocarpus costulatus</i> V. Sl. | Dipterocarpaceae | T | 16 | 63.0 | | |
| Morphotype 1 | Connaraceae | L | 11 | 64.7 | | |
| <i>Alchornea rugosa</i> (Lour.) M.A. | Euphorbiaceae | T | 10 | 66.3 | | |

After 2 y, no differences were found in mortality between experimental and control plots (Figure 1). Tall plants had significantly higher odds of survival than shorter plants ($\chi^2 = 12.05$, $df = 1$, $P < 0.001$), but the odds of survival did not differ between exclosures and controls ($\chi^2 = 0.98$, $df = 1$, $P = 0.32$). In contrast to mortality, the number of recruits in exclosures was three times greater than the number in controls (Figure 1). Seven out of eight exclosures had higher recruitment than their paired control plots, while the eighth exclosure had more recruits than one of its two paired controls. Recruits in exclosures were also slightly taller than recruits in controls (Table 2). Seedling (untagged plants < 30 cm tall) plots within fences had 56% more individuals in 1998 than controls (Table 2). Woody stem density in 1998 was much higher in exclosures (142.3 m^{-2}) than in controls (107 m^{-2}) (Table 2). This difference was the result of large increases in the number of stems in the two smallest size categories: 30–40 and 40–50 cm tall (Figure 2).

Species diversity in 1998, as measured by Fisher's α , was significantly lower in exclosures than in controls (Table 2). Number of species, however, was greater within exclosures (Figure 3). Number of stems and number of species in 1998 were highly correlated in both exclosures ($r^2 = 0.73$) and controls ($r^2 = 0.82$). This relationship did not differ for control and exclosure plots in the

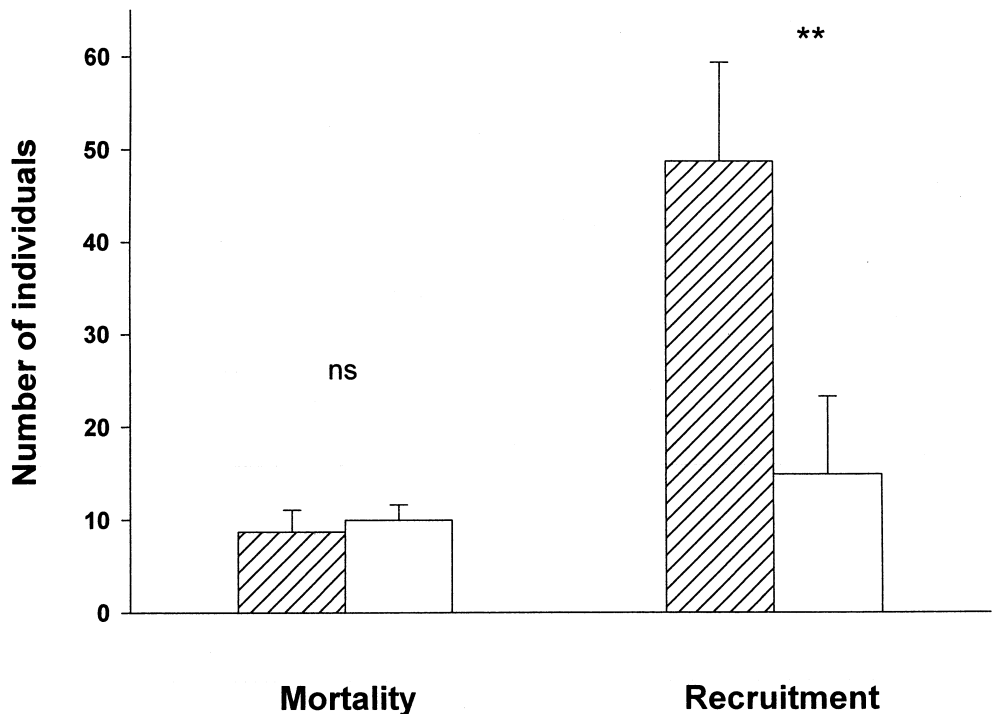


Figure 1. Mean mortality and number of individuals that recruited into the ≥ 30 -cm tall size class for exclosures (hatched bars, $n = 8$) vs. controls (open bars, $n = 16$) in Pasoh Forest Reserve, Malaysia. All values are LS means with the number of stems in 1996 used as a covariate.

Table 2. Results of analyses of variance for treatment effects. Average values are LS means calculated in SAS using PROC MIXED. All variables had a covariate in the ANOVA except height of recruits, number of seedlings and proportion of recruits made up of lianas. For growth rates of the eight species with ≥ 50 stems surviving between surveys, plants which lost more than 10 cm of stem height were deleted from the analyses (17 in total), as was one extreme positive growth outlier for each of three species. The final sample sizes for growth under each treatment are shown in parentheses after the standard errors. Degrees of freedom differ according to the number of plots in which the species was found.

| Variable | LS means \pm SE | | (df) | F | P |
|--|-----------------------|-----------------------|---------|-------|-------|
| | Exclosure | Control | | | |
| Stand structure | | | | | |
| Mortality, 1996–1998 | 8.7 \pm 2.37 | 10.0 \pm 1.67 | (1, 14) | 0.48 | 0.50 |
| Recruits (> 30 cm tall), 1996–1998 | 48.8 \pm 10.6 | 14.9 \pm 8.4 | (1, 14) | 10.61 | 0.006 |
| Height of recruits (cm), 1996–1998 | 36.1 \pm 0.72 | 34.5 \pm 0.59 | (1, 15) | 4.78 | 0.05 |
| Seedlings (< 30 cm tall), 1998 | 117.5 \pm 21.0 | 75.5 \pm 17.8 | (1, 15) | 4.84 | 0.04 |
| Stem density, 1998 | 142.3 \pm 11.3 | 107.1 \pm 8.4 | (1, 14) | 9.26 | 0.009 |
| Species diversity | | | | | |
| Species richness, 1998 | 55.7 \pm 1.05 | 50.6 \pm 1.06 | (1, 14) | 7.24 | 0.02 |
| Fisher's α , 1998 | 39.7 \pm 2.81 | 45.8 \pm 2.31 | (1, 14) | 5.48 | 0.04 |
| Lianas | | | | | |
| Liana proportion of stems 30–100 cm tall, 1998 | 30.5 \pm 2.6 | 25.9 \pm 2.0 | (1, 14) | 2.90 | 0.11 |
| Liana proportion of recruits, 1996–1998 | 36.2 \pm 9.0 | 31.7 \pm 7.7 | (1, 15) | 0.31 | 0.58 |
| Height growth (cm), 1996–1998 | | | | | |
| Trees initially 101–700 cm tall | 19.64 \pm 3.04 | 12.88 \pm 2.41 | 1, 15 | 4.85 | 0.04 |
| Trees initially 30–100 cm tall | 10.09 \pm 1.39 | 8.23 \pm 1.11 | 1, 15 | 1.36 | 0.22 |
| Lianas initially 30–100 cm tall | 9.69 \pm 2.36 | 9.69 \pm 1.84 | 1, 15 | 0.00 | 1.00 |
| Eight most common species, 1996–1998 | | | | | |
| <i>Xerospermum norhanianum</i> Bl. | 6.75 \pm 1.34 (32) | 6.88 \pm 1.09 (52) | (1, 11) | 0.01 | 0.94 |
| <i>Anaxagorea javanica</i> Bl. | 13.18 \pm 1.97 (25) | 10.33 \pm 1.44 (51) | (1, 6) | 1.56 | 0.26 |
| <i>Shorea maxwelliana</i> King | 32.10 \pm 3.97 (17) | 13.12 \pm 4.67 (53) | (1, 8) | 5.09 | 0.05 |
| <i>Caesalpinia parviflora</i> Prain ex King | 11.25 \pm 2.59 (20) | 5.58 \pm 1.59 (39) | (1, 5) | 5.68 | 0.06 |
| <i>Ardisia crassa</i> C.B. Clarke | 5.45 \pm 1.84 (13) | 8.14 \pm 1.11 (36) | (1, 5) | 1.57 | 0.27 |
| <i>Rothmania macrophylla</i> (Hk. F.) Bremek. | 11.32 \pm 2.48 (38) | 7.49 \pm 2.27 (20) | (1, 9) | 1.30 | 0.28 |
| Morphotype 1 | 7.56 \pm 1.93 (15) | 3.83 \pm 1.44 (33) | (1, 11) | 3.20 | 0.10 |
| <i>Rinorea horneri</i> (Korth.) O.K. | 6.10 \pm 1.85 (13) | 6.62 \pm 1.28 (39) | (1, 6) | 0.07 | 0.80 |

1996 survey (ANCOVA, $F = 0.36$; $df = 3, 23$; $P = 0.56$), but was significantly different in 1998 (ANCOVA, $F = 6.44$; $df = 3, 23$; $P = 0.02$); more species accumulated per individual stem in controls ($y = 18.60 + 0.33x$) than in exclosures ($y = 27.74 + 0.18x$).

Overall height growth of stems initially between 1–7 m tall was 50% greater inside exclosures (Table 2). No differences were found for tree stems initially between 30–100 cm tall. Of the eight most common species, three showed marginally significant greater mean height growth in exclosures (Table 2). The other five most common species had similar mean growth increments in each treatment.

No treatment differences were detected in height growth for free-standing lianas initially between 30–100 cm tall (Table 2). No significant differences were found in the proportions of stems between 30 and 100 cm tall made up

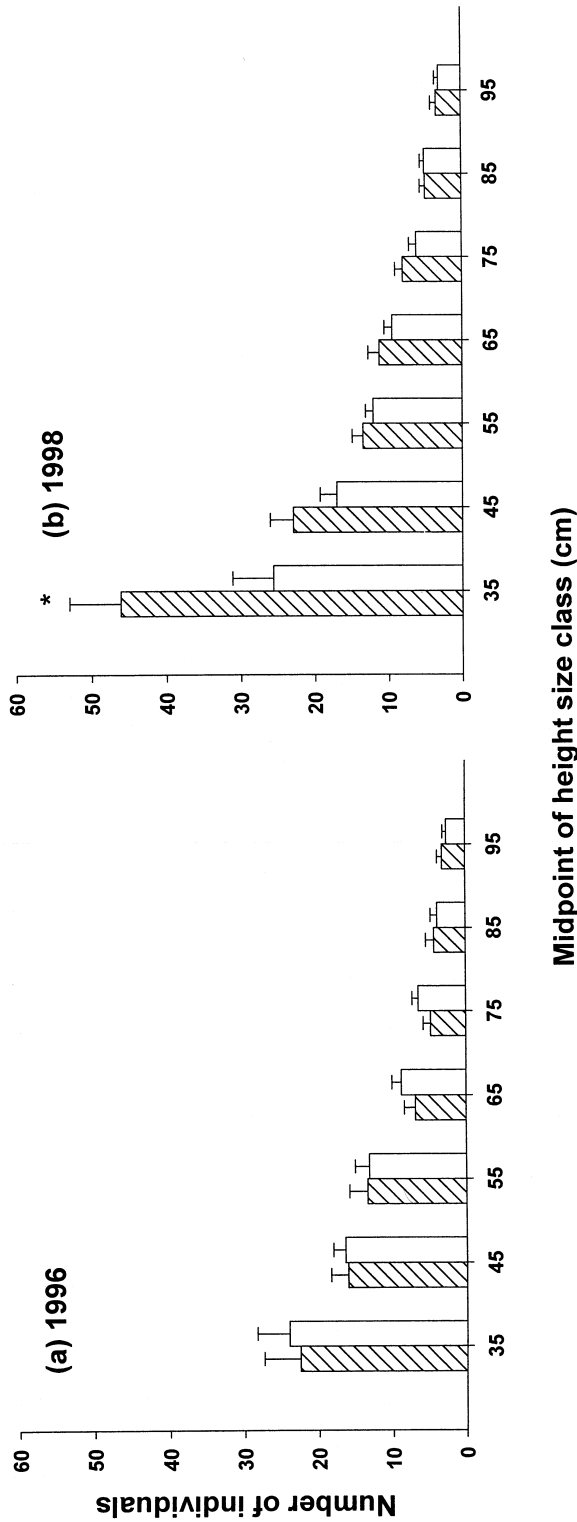


Figure 2. Height size-class histograms of 10-cm increments for plants < 100 cm tall in controls and exclosures from 1996 and 1998. Height classes are represented by the increment midpoint (i.e. 35 represents the height increment from 30–39 cm tall). Number of individuals in the exclosures is the total number of plants in all exclosure plots (hatched bars, n = 8) in a given size class. Number of individuals in the controls is the total number of plants in all control plots (open bars, n = 16) in a given size class divided by 2 to standardize for area. Bars represent 1 S.E.

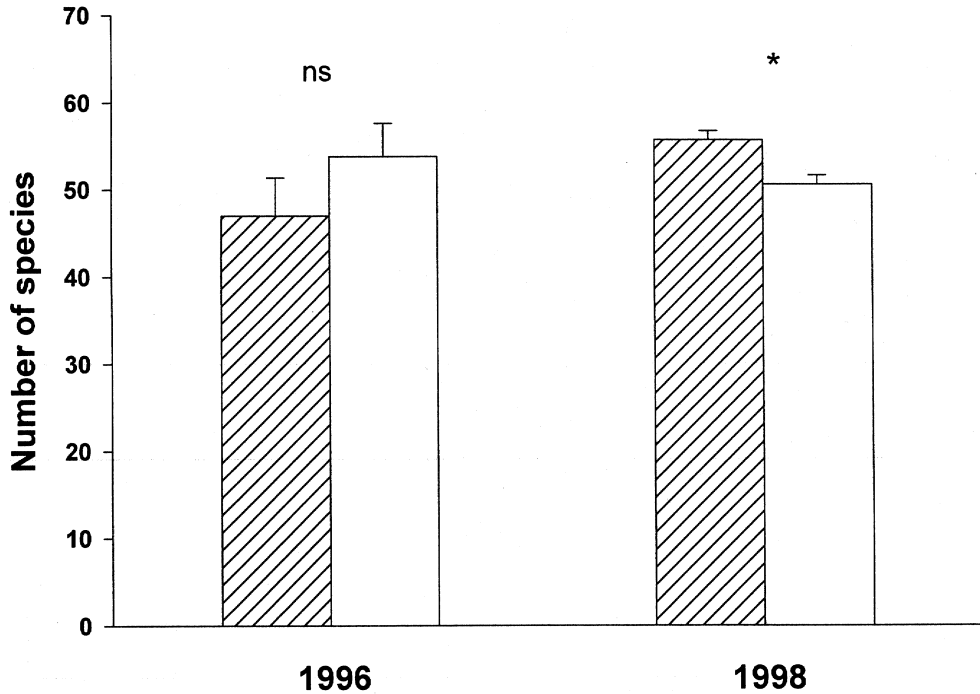


Figure 3. Average species richness values for exclosures (hatched bars, $n = 8$) and controls (open bars, $n = 16$) in 1996 and 1998. The 1998 values are LS means with 1996 values used as a covariate. Bars represent 1 S.E.

by lianas. Nor were differences in liana proportions found among the recruits (Table 2).

DISCUSSION

The net effect of pig exclusion on the understorey woody vegetation at Pasoh Forest Reserve was considerable. After only 2 y in the absence of pigs, the average size of recruits, number of recruits, overall stem density and species richness were all greater inside exclosures than in paired controls. The fact that a mast fruiting event occurred during the first few months of this study probably allowed us to detect such influences over such a relatively short duration. More time is required to see if the observed treatment differences in stem number and diversity persist, are additive over time, or are minimized as a result of compensatory mortality. In the short term, though, it is clear that pigs are having strong impacts on understorey plants at PFR.

Nest building

The exclosures were designed to eliminate all pig activity, including nest building, rooting and seed predation. However, the differences found between

enclosures and controls are not likely due to nest building. During the 2 y of this study, only one nest was built in the research area, about 2 m away from a control plot. Mortality in that control plot was almost twice that of any other plot, but the overall mortality rate between treatments still did not differ significantly. In addition to high mortality in that plot, 22 plants near the nest had negative height growth rates, and at least 12 of these had stems snapped off by a pig for nest construction. Nonetheless, four other plots had similar or higher numbers of stems with negative growth due to factors other than pigs (e.g. plants damaged by branchfall or stem borers). Consequently, nest building appears to have caused little, if any, of the observed differences in the understorey vegetation between treatments. We therefore attribute the differences in this enclosure study to pig rooting and seed predation. Whether differences are due more to rooting or seed predation is impossible to determine here.

Seed predation

Predation of seeds by vertebrates can have profound effects on plant communities. In a dipterocarp forest of Borneo, Curran *et al.* (1999) reported an almost complete lack of woody seedling recruitment over a 10 y period at Gunung Palung National Park. This extraordinary example of seed predation was attributed to the movement of bearded pigs from the matrix of secondary forest that surrounds the park into the park itself for feeding on fallen fruits, as fruit production was much higher in the primary forest. Thus, due to a far-reaching edge effect (Laurance 2000), the relative density of bearded pigs was much higher inside the reserve, with dramatic effects on seed survival and woody plant recruitment. The situation at PFR is similar to that described from Gunung Palung with regard to increased seed predator abundance in the primary forest. Due to an absence of natural predators of wild pigs at PFR, and an intense edge effect in the form of an abundant food supply in the surrounding matrix, the density of *Sus scrofa* in the reserve has increased considerably (Ickes & Williamson 2000). Our study showed that after 2 y recruitment of woody saplings inside enclosures was three times greater than in adjacent control plots. We attribute, in part, the lower recruitment in control plots to vertebrate seed predation. Unfortunately, in our study it is impossible to attribute the seed predation entirely to *Sus scrofa* because the granivorous lesser mouse-deer was also excluded. Nonetheless, given the size differential between pigs and mouse-deer, and the remarkable pig density at PFR, it seems probable that most impacts can be attributed to *Sus scrofa*.

Soil rooting

Pig rooting may also influence understorey plant density and diversity and account to some extent for the findings of this study. In Great Smoky Mountains National Park (GSMNP) in the southeastern United States, rooting by introduced pigs was shown to decrease herbaceous ground cover from *c.* 90 to 10% (Bratton 1975), alter species composition in favour of those with deep or poisonous roots, decrease plant species richness (Bratton 1974) and virtually eliminate

two leaf-litter-dependent vertebrates (Singer *et al.* 1984). As there is little herbaceous vegetation at PFR, the decrease in woody seedling density reported here from Malaysia is comparable to decreases in herbaceous ground cover in the continental USA. Herbaceous cover in the GSMNP returned to normal levels three years after pig exclosures were built, but species richness remained lower than expected (Bratton *et al.* 1982). Mean species richness per plot increased over 2 y in our exclosures while staying roughly the same in controls. Diversity, as measured by Fisher's α , however, was higher in control plots. These seemingly contrasting results are a function of the significant increase in stem density within exclosures without a concomitant increase in new species. On average in 1996, one new species was measured for every three stems, while in 1998 one was measured only for every five stems. Cumulative species richness across plots in 1998 was identical between exclosures and controls. Furthermore, the large increase seen in the number of plants in the two smallest size classes suggests that pigs at Pasoh Forest Reserve are having an unusually strong influence on understorey plant dynamics. As seen in Figure 3, the size class histograms for exclosures in 1998 represent a more typical distribution of plants across increasing size classes, in which there is an abundance of small seedlings.

In addition to changes in cover and composition, pig rooting may also affect plant growth rates. Lacki & Lancia found that the dominant overstorey tree species in GSMNP, *Fagus grandifolia*, showed increased shoot elongation in areas rooted by pigs. In this study, a difference was found in overall height growth for trees initially between 1–7 m tall in rooted vs. unrooted plots, but plants in exclosures grew more. These data are in contrast with the positive effects of pig rooting on growth rates for *Fagus grandifolia*. Pig rooting, however, may have different impacts on different species. Response differences may depend on variables such as tree size, root growth patterns and mycorrhizal associations. Also, Lacki & Lancia (1986) measured shoot elongation in large trees of a species-poor forest. Our study, in contrast, measured height growth in understorey plants in an exceptionally diverse area. Finally, it should be noted that the mean growth rates were quite low in the Malaysian understorey. It is possible that growth response to pig exclusion is stronger than documented here, but that more than 2 y are needed to detect such differences in understorey conditions.

Pig rooting may also induce plant mortality, but in a manner unable to be detected with our experimental design. All susceptible individuals might already have died prior to our initial survey because pigs seem to root the same areas repeatedly at PFR and may have been doing so for years. Roughly half of the plots appeared to be thoroughly disturbed by rooting in 1996. Consequently, in 1998 we only would have detected impacts of rooting on seedling mortality where pigs rooted previously undisturbed control plots.

Effects on free-standing lianas

Lianas composed a high percentage of total, free-standing woody stems < 200 cm tall (25.6%) and of stems between 30 and 50 cm tall (31.9%) at PFR.

Although these figures are higher than those reported for lowland neotropical sites (Putz 1983, 1984; S. Schnitzer & W. Carson, unpubl. data), they are not unusual for aseasonal dipterocarp forests in Southeast Asia (Putz & Chai 1987), and we found no evidence to support the hypothesis that pig rooting alters the proportion of small woody stems composed by lianas.

Conclusions

This study documented that native pigs play an important role in plant dynamics at the understorey level in this Malaysian rain forest. Pigs affected stem density, species richness, growth and possibly mortality. Although the current density of pigs at PFR is certainly higher than historical levels, an entire suite of large-bodied herbivorous mammals is completely absent from the study area. Although we are unaware of any studies documenting the effects on the understorey of large mammals such as deer, elephants, rhinos, wild cattle and tapirs on tropical vegetation in Southeast Asia, their impacts may be considerable. How the effects of pigs at their current density at PFR compare with those of a complete suite of terrestrial herbivores is difficult to determine. Nonetheless, these results are relevant for numerous other small forest reserves and fragments in Southeast Asia, where local extinction of predators and large herbivores has occurred.

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