



The Influence of Soil Type on Rain Forest Insect Herbivore Communities

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ABSTRACT

Insect herbivores were collected from five species of dipterocarp tree seedling within a large-scale reciprocal transplant experiment in Sabah, Malaysia, on alluvial and sandstone soils in both gap and understory plots. The aim was to determine whether the location and ecological specialization of seedlings influenced the herbivore communities found on and around them. Three major groups of folivores were collected: Coleoptera, Orthoptera, and larval Lepidoptera. Herbivory of all species was confirmed through laboratory trials. Herbivore abundance in the understory plots was extremely low relative to the gaps. Rank-abundance curves were similar on both soil types, differing only within the Lepidoptera. Coleoptera and Orthoptera communities were numerically dominated by a small suite of species capable of feeding on all dipterocarp species tested, whereas lepidopteran communities had both greater species richness and diversity. When corrected for leaf area surveyed, the abundance of Coleoptera was similar on both soil types, while larval Lepidoptera were more abundant in sandstone plots and Orthoptera were more abundant in alluvial plots. Estimated species richness of all three taxa was greater in alluvial forest, but there were contrasting patterns in Simpson diversity and evenness between groups. Species richness of Lepidoptera was greatest on seedlings when grown in their native soil type, providing partial evidence for possible escape effects, although this was not matched by differences in folivore abundance. The link between herbivore communities and herbivory rates on rain forest tree seedlings is complex and is unlikely to be detected through simplistic measures of abundance, species richness, or diversity.

Key words: Borneo; Coleoptera; dipterocarp; diversity; folivores; Lepidoptera; Orthoptera; reciprocal transplant.

IN TROPICAL FORESTS, INSECT HERBIVORES IMPOSE STRONG SELECTIVE PRESSURES on plants, their impact exceeding that of larger vertebrates (Janzen 1981, Clark & Clark 1991). Their communities are often described as hyperdiverse, with extraordinary species richness defying attempts at comprehensive sampling. Species accumulation curves seldom, if ever, reach asymptotes (Novotny & Basset 2000, Gotelli & Colwell 2001, Lucky *et al.* 2002). Identifying the causes and consequences of this high diversity are among the greatest challenges facing tropical ecologists.

Species richness is the simplest and most common means of describing the ecological diversity of a community (Magurran 2004), although its estimation is contentious, with the accuracy dependent upon habitat heterogeneity and sampling effort (Gotelli & Colwell 2001). In complex environments, such as forests, the species richness of insect herbivores may be particularly sensitive to ecological variation on small scales (Marquis 1991). Basset (1996) found that most of the variation in insect species richness on 10 species of tree in Papua New Guinea was due to local factors, including the availability of food resources and abundance of natural enemies, rather than broader processes such as the host tree's taxonomic isolation, geographical distribution, or habitat range.

There have been few controlled comparisons of insect herbivore communities between habitats within forests, for example

contrasting soil types or light conditions. Basset *et al.* (2001) found increased herbivore abundance in response to newly formed gaps, and other studies have confirmed that their abundance increases in high-light environments (Coley 1983, Aide & Zimmerman 1990, Marquis & Braker 1994, Richards & Coley 2007). Tropical insect communities also change seasonally, with increased abundance in the wet season, even if the dry season is not pronounced (reviewed in Wolda 1978). In both cases, this may be a response to the increased availability of developing leaves, the preferred resource for many herbivore species.

The insect herbivore community found upon a given plant species may also be affected by the location of any single plant. We would anticipate that individual plants would support a greater species richness of herbivores in their native habitat type since the density of their conspecifics will be greatest there. This is one expectation of the 'escape hypothesis' (Janzen 1970, Connell 1971). It has been shown that the species richness of herbivores on a tropical shrub is related to the local abundance of that species (Marquis 1991), although this is not a reliable indicator of their impact (Marquis 1991, Marquis & Braker 1994).

It has been suggested that species in tropical ecosystems occupy narrower niches than those in temperate regions, resulting in greater overall species richness on a habitat scale (MacArthur 1969). Niche size of insect herbivores is most conveniently defined by dietary breadth, leading to the common presumption that most tropical insect herbivore species are specialists, a concept subject to much debate (Fiedler 1998, Novotny & Basset 2005, Dyer *et al.* 2007).

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Most studies have focussed on folivores (leaf chewers) and sap-feeders, and although host specificity may be greater for concealed feeders such as leaf-miners, gall makers, or stem and shoot borers (Basset 1992), their diversity is as yet poorly understood.

The aims of this study were to describe the insect folivore communities present on seedlings in a large-scale reciprocal transplant experiment across two soil types in a Bornean rain forest (see Eichhorn *et al.* 2006) and to assess whether they differed in structure, abundance, species richness, and diversity. We predicted that seedling species would support a greater species richness and abundance of herbivores on their native soil type.

METHODS

STUDY SITE.—The Kabili-Sepilok Forest Reserve (5°10' N, 117°56' E), Sabah, Malaysia, consists of 4294 ha of coastal mixed-dipterocarp rain forest surrounded by a matrix of cultivation and secondary forest. Alluvial and sandstone soils support forests differing in structure and species composition. Alluvial forests are dominated by canopy trees of *Parashorea tomentella* (Sym.) Meijer, *Shorea johorensis* Foxw. (Dipterocarpaceae) and *Eusideroxylon zuwageri* Teijsm. & Binn. (Lauraceae), while sandstone forests are dominated by *Shorea multiflora* (Burck) Sym., *S. beccariana* Burck and *Dipterocarpus acutangulus* Vesque (Dipterocarpaceae). For a full description, see Fox (1973). Mean annual precipitation is 2929 ± 134 mm (mean \pm SE; data from 1976 to 1995) of which 45 percent falls between November and February (Fox 1973) with no single month below 100 mm on average.

EXPERIMENTAL DESIGN.—The study took place as part of a long-term large-scale reciprocal transplant experiment (Eichhorn *et al.* 2006). Seedlings of five species of dipterocarp tree were selected to investigate the effects of habitat specialization on their responses to different environmental conditions and biotic interactions. Two of the species are restricted to alluvial soils within the reserve (*Hopea nervosa* King, *P. tomentella*), while another (*Shorea fallax* Meijer) does not occur in the reserve but is elsewhere confined to alluvial soils. Two further species occur locally only on sandstone soils (*S. multiflora*, *Hopea beccariana* Burck). Seedlings were planted in 10 sites, five in alluvial lowland forest and five on sandstone ridges, between March and June 2000. Each site consisted of two paired plots, one in a natural treefall gap and another in the adjacent understory. Each plot contained 150 seedlings from the five species in a randomized block design. A complete fertilizer was applied biannually to half of the seedlings.

INSECT COLLECTION.—Insects were sampled between 17 May and 14 July 2001, which was considered to be the dry season, and from 18 January to 6 March 2002, regarded as the wet season. Thirty seedlings were randomly selected within each gap and understory plot from those not included in the herbivory assessments (Eichhorn *et al.* 2006): six of each species, half from the fertilizer treatment. Understory plants were randomly selected from those with more than four mature leaves, although it was occasionally necessary to

survey more than six seedlings to permit a minimum sample size of 24 leaves. No plant was visited more than once in any season. Additional seedlings were added to account for mortality between collection periods. Gap plots were surveyed between 0630 h and 1300 h, understory plots from 1200 h to 1400 h. Seedlings were comprehensively hand-searched and all live insects were collected. The survey was nondestructive apart from the removal of leaves with mines or leaf rolls. Orthopterans were collected by sweep-netting around the edges of the gap plots, standardized as a single circuit within one sweep of the seedlings (*ca* 1.5 m). Sweep-netting was abandoned in the understory due to very low orthopteran abundance.

Feeding on the study plants was confirmed through laboratory trials that tested responses to both mature and developing leaves. Species that did not feed were excluded, although it is possible that they may have fed on parts other than the leaves. Larval lepidopterans were reared to adulthood on their preferred leaf type. Coleopterans and orthopterans were tested in cafeteria trials with leaf segments of the five experimental species plus two additional dipterocarps, *Shorea leprosula* Miq. and *Dryobalanops lanceolata* Burck, to determine their dietary breadth (for additional details see Eichhorn *et al.* 2007). Specimens were sorted into morphospecies in September and October 2002. Samples were sorted simultaneously to ensure morphospecies designations were independent of sample date or habitat.

SAMPLING EFFORT.—Sampling effort was measured in terms of number of individuals per: (1) plot; (2) 1000 leaves; and (3) total leaf area surveyed, to capture different scales of variation. Seedling and leaf sizes varied considerably between species and treatments and therefore estimates of species turnover were not possible. Numbers of leaves on individual plants at time of sampling were estimated from data collected by R. Nilus (unpubl. data) and leaf sizes were measured by D. H. Dent (unpubl. data). Sampling effort for orthopterans was considered equal for all gap plots. No orthopterans were captured in the understory.

STATISTICAL ANALYSIS.—Collections made on fertilized and unfertilized seedlings were grouped within seedling species. There was no evidence for variation between fertilized and unfertilized seedlings in rates of herbivory (Eichhorn *et al.* 2006), foliar nitrogen content (D. H. Dent, unpubl. data) or phenolic defences (M. P. Eichhorn, unpubl. data), and consequently there is no basis for believing that their insect communities were likely to differ appreciably. A preliminary analysis indicated that abundance of dipterocarp-feeding insects was not affected by fertilization.

Diversity analysis was conducted in Species Diversity and Richness v.3.0 (PISCES Software). Species richness within groups of samples was estimated using the nonparametric Chao2 method that is relatively robust and accurate even at low sample sizes (Colwell & Coddington 1994). Means and standard errors were calculated from 50 iterations. Diversity was measured according to the Simpson index D , is presented as $1/D$, and was transformed prior to statistical analysis as $-\ln D$, which is independent of sample size (Rosenzweig 1995). The Simpson evenness measure $E_{1/D} = (1/D)/S$ where S is the number of species in the sample (Smith & Wilson 1996).

Analysis of differences in folivore abundance between species followed a mixed-effects model procedure in R 2.4.1 with the effect of plot included as a random factor.

RESULTS

Approximately 60,000 leaves were surveyed, of which 90 percent were on gap plants. Three major folivore groups occurred—Coleoptera, Orthoptera, and Lepidoptera. Small numbers of Phasmodidae were collected, but they invariably selected leaves of *S. leprosulula* in preference trials and were reluctant feeders on other dipterocarp species. Since this species was not used in the experiment, they were not considered further. The results for each of the major taxonomic groups of insect folivores are presented in turn.

COLEOPTERA.—Eighty-five morphospecies were identified, of which 32 were weevils (Curculionioidea) and 29 leaf beetles (Chrysomeloidea). More than two-thirds (58 species) were recorded only as singletons. Although only 18 species (21% of total) were confirmed as feeders, in terms of abundance, known dipterocarp feeders made up 78 percent of all beetles collected. Only one known dipterocarp-feeding species was collected from the understory in the entire course of the sampling. Since their abundance in the understory was so low, they are excluded from analyses.

The community was dominated by folivore species capable of feeding on all five dipterocarp species in feeding trials. The five most abundant species overall were all weevils, comprising > 90 percent of all individuals collected. A single species (*Epicalus* sp.) made up 64 percent of all beetles collected in the alluvial forest. In contrast, species found as singletons comprised only 1.6 percent of individuals.

There was no significant difference between the rank/abundance plots on the soil types (Kolgorov–Smirnov two-sample test, $W = 13.8$, $P > 0.10$; Fig. 1A). Far greater numbers of individuals were collected in the alluvial forest than the sandstone (Table 1; Fig. 1A). Although the abundance of coleopterans was greater in the alluvial gap plots ($F_{1,8} = 22.8$, $P = 0.001$; Table 1), this effect was absent when considering the abundance per 1000 leaves or per unit leaf area. Using a mixed model approach, there were no significant differences in abundance of coleopterans per unit leaf area between species ($\Delta d = 1.69$, $df = 1$, $P = 0.193$) or soil types ($\Delta d = 0.23$, $df = 1$, $P = 0.625$) and no interaction between species and soil types ($\Delta d = 1.64$, $df = 1$, $P = 0.199$). A greater estimated species richness was found in the alluvial forest (Fig. 1B) as well as an increased Simpson diversity ($F_{1,7} = 6.95$, $P = 0.032$), although evenness did not differ between soil types ($F_{1,7} = 0.327$, $P = 0.585$; Table 2); one sandstone plot was excluded as it only contained a single species.

ORTHOPTERA.—Almost all individuals were collected in gaps. A total of 39 morphospecies were identified, of which 33 were crickets (Ensifera) and six were grasshoppers (Caelifera). An undetermined number of Tettigidae (Caelifera) species were also recorded, but

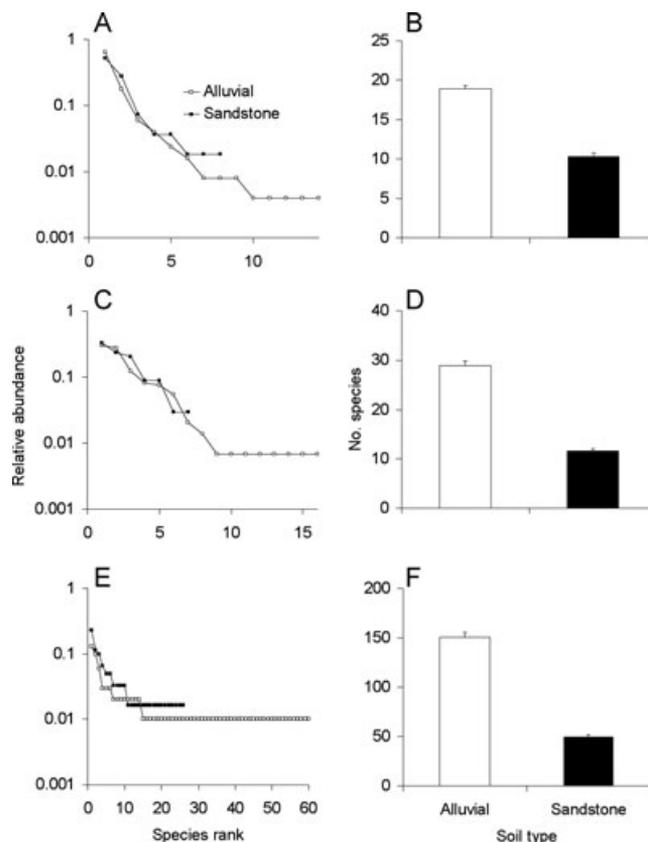


FIGURE 1. Whittaker rank/abundance plots and estimated species richness for insect herbivore communities in experimental plots on alluvial and sandstone soils; (A, B) Coleoptera, (C, D) Orthoptera, (E, F) Lepidoptera. Species richness estimated using Chao2; means \pm SE from 50 iterations.

these showed no inclination to feed on dipterocarps and were discarded. Confirmed dipterocarp feeders made up 63.5 percent of the collection. Only 16 species of cricket were confirmed as feeding on dipterocarps, along with all six species of grasshopper (excluding Tettigidae). Species collected as singletons made up only 3.9 percent of the feeding individuals.

As with the Coleoptera, no significant difference between the rank/abundance plots was found between soil types ($W = 9.41$, $P > 0.10$), and a greater number of Orthoptera were collected in the alluvial forest (Table 1; Fig. 1C). The estimated species richness in the alluvial forest was more than twice that in the sandstone (Fig. 1D). There were no significant differences between soil types in Simpson diversity ($F_{1,8} = 0.127$, $P = 0.731$) or evenness ($F_{1,8} = 2.38$, $P = 0.161$; Table 2).

LEPIDOPTERA.—Larvae of 76 species were successfully reared through to adults. For some groups (e.g., Limacodidae, Geometridae), the larval stages were sufficiently distinctive that they could be recorded as additional species. All larvae were assumed to be dipterocarp feeders, as all fed in the laboratory, were observed feeding

TABLE 1. Abundance of three main insect groups in gap plots according to three measures of sampling effort. Means per plot \pm SE with ANOVA; significant test results in bold. Orthoptera were collected by sweep-netting at plot edges and sampling effort was considered equal between plots.

Group	Per plot			Per 1000 leaves			Per m ² foliage		
	Alluvial	Sandstone	<i>P</i>	Alluvial	Sandstone	<i>P</i>	Alluvial	Sandstone	<i>P</i>
Coleoptera	32.1 \pm 4.8	6.9 \pm 2.1	0.001	6.6 \pm 1.3	4.8 \pm 1.4	0.357	1.6 \pm 0.3	1.6 \pm 0.4	0.954
Orthoptera	38.4 \pm 6.1	8.4 \pm 1.1	0.001	–	–	–	–	–	–
Lepidoptera	55.4 \pm 18.1	35.2 \pm 21.4	0.146	7.4 \pm 3.6	14.0 \pm 5.9	0.065	2.8 \pm 0.6	8.7 \pm 3.4	0.006

TABLE 2. Simpson's diversity index $1/D$ and evenness measure $E_{(1/D)}$ for the three main groups of insect folivores. Means per plot \pm SE with ANOVA or Mann-Whitney *U*-tests on $-\ln D$; significant test results indicated in bold.

Group	$1/D$			$E_{(1/D)}$		
	Alluvial	Sandstone	<i>P</i>	Alluvial	Sandstone	<i>P</i>
Coleoptera ^a	0.50 \pm 0.06	0.28 \pm 0.05	0.032	0.09 \pm 0.01	0.07 \pm 0.02	0.585
Orthoptera	0.17 \pm 0.01	0.17 \pm 0.04	0.731	0.02 \pm 0.00	0.04 \pm 0.02	0.161
Lepidoptera	0.06 \pm 0.01	0.14 \pm 0.03	0.030	<0.01 \pm 0.00	0.02 \pm 0.00	0.016^b

^aOne sandstone plot excluded as it only contained a single species.

^bMann-Whitney *U*-test.

in the field, or had pupated near obvious patches of feeding activity. No species was consistently associated with a single host plant. Larvae from gaps made up 95.4 percent of all those collected; the small numbers in the understory preclude any further analysis. Two species were only found in the understory; in both cases these were singletons in the alluvial forest.

Unlike the previous two folivore groups, rank/abundance plots differed between the two soil types ($W = 530.4$, $P < 0.05$; Fig. 1E). There was no difference in the numbers of larvae collected in the alluvial and sandstone forest gaps (Table 1; Fig. 1E), although there was a tendency for alluvial plots to contain greater numbers. This effect was reversed when considering larvae per 1000 leaves, and indeed the numbers of larvae per unit leaf area were greater on sandstone soils ($F_{1,8} = 13.4$, $P = 0.006$; Table 1). Using a mixed model approach, there were no significant differences in abundance of lepidopterans per unit leaf area among species ($\Delta d = 1.34$, $df = 1$, $P = 0.247$) and no interaction between species and soil types ($\Delta d = 1.48$, $df = 1$, $P = 0.223$), but the differences among soil types remained clear ($\Delta d = 4.70$, $df = 1$, $P = 0.030$).

Estimated species richness in the alluvial forest was more than twice that in the sandstone (Fig. 1F). Sandstone forest gaps had greater Simpson diversity ($F_{1,8} = 6.89$, $P = 0.030$) and evenness ($F_{1,8} = 8.22$, $P = 0.016$; Table 2), although this was still extremely low. Comparing among host species, the estimated species richness of lepidopteran herbivores was greater on the three alluvial specialists (*H. nervosa*, *P. tomentella*, and *S. fallax*) when grown on alluvial soils, and on the two sandstone specialists (*S. multiflora* and *H. beccariana*) in the sandstone forest (Fig. 2).

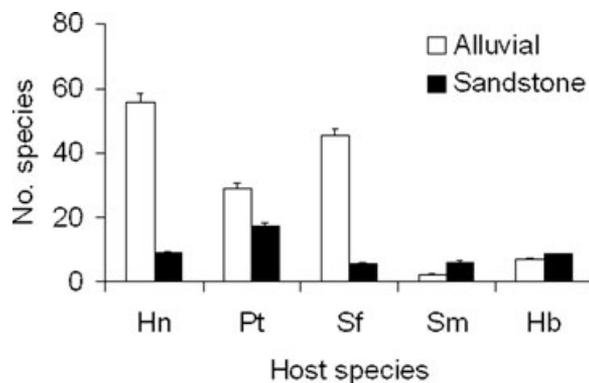


FIGURE 2. Estimated number of lepidopteran species feeding upon each of five species of dipterocarp tree seedling. Species richness estimated using Chao2; means \pm SE from 50 iterations. Hn = *Hopea nervosa*; Pt = *Parashorea tomentella*; Sf = *Shorea fallax*; Sm = *Shorea multiflora*; Hb = *Hopea beccariana*.

DISCUSSION

HERBIVORE COMMUNITY STRUCTURE.—Communities of Coleoptera and Orthoptera on both soil types were dominated by relatively few species, with feeding habits that were apparently generalized within the Dipterocarpaceae. Even among the Lepidoptera, no insect species was reliably associated with a single species from among the seven used in cafeteria trials. It would appear that the insect herbivore communities in this system are largely composed

of abundant oligophages, at least upon the dipterocarp trees that dominate these forests.

The rank species abundance curves for the Coleoptera and Orthoptera are remarkably similar, reflecting a comparable community structure between the two taxa and over the two soil types (Fig. 1A, C). Only the Lepidoptera community structures differed between soil types (Fig. 1E) due to greater relative abundances of lower order species in the sandstone plots.

Dipterocarp-feeding species collected as singletons comprised only 1.6 percent of the Coleoptera collected and 3.9 percent of the Orthoptera. It is likely that many more singletons were dipterocarp feeders but failed to feed in the single trial they received. It is also probable that some species fed on parts of plants other than the leaves. Despite their abundance in the plots, leaf beetles (Chrysomelidae) would seem to be a minor component of the dipterocarp herbivore community, although they formed a large proportion of the nonfeeding species.

Collections of tropical insect herbivores typically produce species abundance curves with several highly abundant species and a long tail collected only as singletons (Novotny & Basset 2000, Lucky *et al.* 2002, Novotny *et al.* 2002). These species are not necessarily rare within the forest as a whole, since the tendency of studies to concentrate on only a few focal plant species does not preclude the possibility that particular herbivores may be more abundant on other plant species (Novotny & Basset 2000). Lepidopteran assemblages on trees in Papua New Guinea were dominated by a small number of species with broad feeding habits (Novotny *et al.* 2002), with a single species forming almost half of the individuals and total biomass. Dominance of a small group of generalized feeders appears to increase with successional stage of the plant community (Leps *et al.* 2001). In contrast, considering a wide range of herbivore taxa, Novotny and Basset (2000) collected 278 of 1050 species (26%) only as single individuals, making up only 0.3 percent of all individuals collected. A high richness of such rare species is likely to be unimportant in terms of the impact on a given plant species, regardless of their dietary range.

The classical view of tropical rain forest insect herbivores is that they are highly specialized in their feeding, permitting a large number of niches and coexisting species (MacArthur 1969, Dyer *et al.* 2007), although other evidence suggests that tropical and temperate insect herbivores are similar in their dietary breadth (Novotny & Basset 2005). Furthermore, a high species richness of trees over small spatial scales ought also to promote the evolution of generalized feeding, especially in groups with limited dispersal capabilities, such as weevils. In general, the importance of specialist herbivores in driving patterns of herbivory in tropical forests may have been overstated, provoked by the search for Janzen-Connell processes that might drive density- and distance-dependent patterns of herbivore-induced mortality (Janzen 1970, Connell 1971). In this system, the oligophages appear to be a dominant force whose feeding preferences have been linked to differences in herbivory rates between species (Eichhorn *et al.* 2007). The numerical preponderance of generalist or oligophagous species in this and other studies suggests that their impact deserves greater attention.

ABUNDANCE.—Despite the apparently greater abundance of all three groups in alluvial forests (Table 1; Fig. 1), accounting for the amount of foliage sampled revealed interesting differences among the three major taxa. Although more beetles were found per plot in the alluvial forest, there were no significant differences in abundance per unit leaf area. In contrast, lepidopteran larvae occurred at a greater density on sandstone soils. This may reflect aggregated oviposition preferences by adults, which may lay egg batches of similar size on individual seedlings (Strong *et al.* 1984), leading to an equivalent number of larvae per plot but a greater density per unit leaf area when plants differ in size. No such correction is necessary for the Orthoptera, which have markedly greater abundance in alluvial forest, probably attributable to the generally higher density of herbaceous material surrounding the gaps.

Within this system there appear to be no consistent differences in leaf herbivory rates between the two soil types (Eichhorn *et al.* 2006). Previous work has suggested that the abundance of Coleoptera and Lepidoptera is linked to differences in herbivory rates among species in alluvial gap plots (Eichhorn *et al.* 2007), but the variation in lepidopteran density between the two soil types is evidently not driving markedly increased damage rates on sandstone soils. It is also instructive to note that, for both groups, the correction for leaf area results in no discernable differences in density of herbivores on the foliage of the five species, with no evidence of habitat-specific effects. This is consistent with the impression of a community dominated by generalist herbivores distributing themselves among a number of species. In a similar study of the impacts of rain forest herbivory across two soil types, Fine *et al.* (2006) found the same diversity and abundance of insects in gaps for a number of herbivorous groups, although herbivory on test seedlings was not confirmed for any species.

Herbivores are generally more abundant in high light environments than in the understory (Coley 1983, Aide & Zimmerman 1990, Marquis & Braker 1994, Basset *et al.* 2001), as confirmed by the present study. In over 1200 assessments of individual understory seedlings, no confirmed dipterocarp-feeding Orthoptera species and only one Coleoptera were collected. This is extremely unlikely to be a mere artefact of sample size caused by the differences in seedling size. The abundance of lepidopterans would appear to be slightly greater, although they formed fewer than 5 percent of the collections overall. This does not correspond with the similar herbivory rates for both mature and new leaves in gap and understory habitats (Eichhorn *et al.* 2006), suggesting that a simplistic association between the two cannot be assumed. In a comparable study, Richards and Coley (2007) found higher abundance of herbivores in gaps and noted a correspondingly greater herbivory rate, although this was due to the inclusion of light-demanding species in the assessment of gap herbivory rates, and no overall differences in rate were found for those species grown in both habitats.

SPECIES RICHNESS.—The species richness of Lepidoptera, as calculated using Chao's presence/absence estimator, was substantially greater than for the other two taxa, while all groups had greater species richness in the alluvial forest (Fig. 1). This parallels the

greater species richness of trees on alluvial soils (Fox 1973). Some caution is required when making comparisons between insect groups due to the different collection technique applied to the Orthoptera and that for the Lepidoptera many species were seldom collected or successfully reared. Nevertheless, the broad pattern is clear.

In general, the alluvial dipterocarp species were fed upon by a greater species richness of Lepidoptera than the sandstone species (Fig. 2). The three alluvial species had a higher estimated species richness of lepidopteran herbivores in the alluvial forest, and the two sandstone species had higher species richness in the sandstone forest (Fig. 2) although in the case of *H. beccariana* the difference is marginal. This finding supports our expectation that more species would feed upon a species where the density of its conspecifics is greatest. That no similar effect was found for the other groups may indicate a limitation in the dispersal and oviposition of lepidopteran adults relative to widespread oligophages in the other taxa. It is a common finding that species richness of herbivores on a given plant species is determined by its abundance within the habitat (*e.g.*, Gilbert & Smiley 1978, Marquis 1991). This cannot be the case for the nonnative species *S. fallax*, however, which must have features that make it palatable to local species. Of the five experimental species, it was the one most preferred by generalist herbivores in feeding trials (M. Eichhorn, unpubl. data) and suffered the greatest damage rates in the field (Eichhorn *et al.* 2006).

DIVERSITY.—The three groups differed in Simpson diversity between soil types—Coleoptera were more diverse in alluvial forests, Orthoptera were similar, and Lepidoptera had higher diversity in sandstone forests (Table 2). Overall, the highest Simpson diversity was recorded for Coleoptera communities, followed by the Orthoptera, with Lepidoptera communities having generally low diversity scores. Evenness of lepidopteran communities increased on sandstone soils, while no difference was detected in the other groups (Table 2), although the evenness scores were remarkably low overall. Once again, these differences did not correspond with any variation in herbivory rates between species or soil types (Eichhorn *et al.* 2006).

CONCLUSIONS.—Insect herbivore communities on dipterocarp seedlings were numerically dominated by a few highly abundant oligophagous species. These are likely to have the greatest impact on the seedlings overall. Although species richness of Lepidoptera was greater on seedling species grown in their native soil type, no such patterns were observed for foliar abundance of either Lepidoptera or Coleoptera, and no parallel exists with previously measured herbivory rates. These findings suggest that gross measures of abundance, species richness, and diversity of insect herbivores are unlikely to assist in explaining the rates and impact of herbivory in tropical forests.

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