Community structure of pre-dispersal seed predatory insects on eleven *Shorea* (Dipterocarpaceae) species

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Abstract: The Dipterocarpaceae in South-East Asia are known for their strict mast fruiting. During fruiting, pre-dispersal seed predation by insects contributes to mortality of dipterocarp seeds. We documented the community structure of insect seed predators on 11 *Shorea* species in Peninsular Malaysia. Fruits were sampled sequentially throughout seed development, and 2144 and 1655 individuals of seed predator weevils and moths were collected in two mast-fruiting events. Four weevils: *Nanophyes shoreae*, nanophyid sp. 1, *Alcidodes dipterocarpi* and *Alcidodes humeralis*, and one moth *Andrioplecta shoreae* were abundant in seeds of the *Shorea* species. The proportion of *N. shoreae* to the total predators became larger in the latter fruiting event than the former while that of *Alcidodes* spp. became smaller. The predator species composition changed during seed development; nanophyid spp. emerged from immature fruits while *Alcidodes* spp. emerged from mature fruits. *Andrioplecta shoreae* emerged from both immature and mature fruits. The level of host specificity measured by Kullback–Leibler distance was low for most predator species in both events. Predator species composition of many *Shorea* was similar to each other due to the dominance of *N. shoreae* though it might gradually differ with the phylogenetic distance between hosts. In conclusion, predator species composition of *Shorea* varied during seed development within a host rather than among hosts. Intermittent synchronized fruiting by congeneric *Shorea* trees would be advantageous to avoid pre-dispersal insect seed predators, and contribute to their reproduction.

Key Words: *Alcidodes*, *Andrioplecta*, dipterocarp, general flowering, masting, Nanophyidae, pre-dispersal seed predation, predator satiation

INTRODUCTION

Seeds are the principal means of reproduction and dispersal for most vascular plants (Vander Wall *et al.* 2005), but seeds are also the stage when the plants are susceptible to heavy predation by animals (Janzen 1971). Therefore, seed predators can affect the population dynamics of individual plant species, and ultimately, diversity and species composition of plant communities (Lewis & Gripenberg 2008).

Many plant species are known to synchronize their flowering or fruiting phenology and vary the amount of crop year to year (van Schaik *et al.* 1993). The intermittent production of large seed crops by a population of plants is called mast seeding or mast fruiting (Kelly 1994). Because of the variations in availability, seeds might be unreliable resources to the predators.

The Dipterocarpaceae, the dominant family in lowland rain forests of South-East Asia, present one of the extreme examples of mast fruiting; they flower synchronously among many species at irregular intervals from 2 to 10 y while few trees flower in years between the events (Appanah 1985, Ashton *et al.* 1988, Numata *et al.* 2003, Sakai 2002). Several hypotheses both in terms of the proximate and the ultimate cause have been proposed to explain the mechanisms of general flowering. The proximate cause is the environmental cues that trigger

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flowering. An increase in sunshine hours (Ng 1977), a drop in night-time temperature (Ashton *et al.* 1988, Yasuda *et al.* 1999), or prolonged droughts (Brearley *et al.* 2007, Medway 1972, Sakai *et al.* 2006) have been proposed. The ultimate cause is the adaptive significance for the evolution of synchronous flowering and/or fruiting, e.g. seed predator satiation (Janzen 1974), pollination enhancement (Sakai *et al.* 1999), resource matching (Kelly 1994), and environmental prediction (Kelly 1994, Williamson & Ickes 2002). Among them, the most plausible and well-known explanation is seed predator satiation (Curran *et al.* 1999). This hypothesis suggests that the mast fruiting of the Dipterocarpaceae is an adaptive strategy for starving their seed predators during non-fruiting periods, while satiating them during synchronous mast-fruiting events.

During the fruiting event, huge amounts of seed are initiated, however, most seeds die prior to full maturation or germination. Aside from the heavy abortion soon after flowering, the main mortality factor is predation by insects or vertebrates and infestation by fungi (Curran & Leighton 2000, Curran & Webb 2000, Maycock *et al.* 2005, Sun *et al.* 2007). Among them, pre-dispersal seed predation by insects is common (Maycock *et al.* 2005, Naito 2008, Sun *et al.* 2007) and has a negative effect on viable seed production (Nakagawa *et al.* 2005).

Most insect seed predators of dipterocarps are weevils (e.g. Curculionidae or Nanophyidae: Coleoptera), moths (e.g. Tortricidae or Pyralidae: Lepidoptera), and barkbeetles (Scolytidae: Coleoptera) (Chey 2002, Daljeet-Singh 1974, Nakagawa *et al.* 2003, Toy 1988). Weevils and moths oviposit in the seeds and on fruits, respectively, when fruits are still on the tree. Normally a single larva grows up in the seed and feeds on its cotyledons, thereby killing the seed (Daljeet-Singh 1974, Toy 1988). Bark beetles attack fruit on the ground, though some possibly attack fruit on the tree, and lay a number of eggs in a seed. Hatched larvae, as well as adult beetles, tunnel into the seeds and feed voraciously (Chan 1977, Daljeet-Singh 1974, Momose *et al.* 1996).

Although insect seed predators are often considered to be highly host-specific, especially in the tropics (Janzen 1980), dipterocarp predators are known to feed on multiple hosts belonging to different genera or even other families (Lyal & Curran 2000, 2003; Nakagawa *et al.* 2003, Robinson *et al.* 2001). However, most previous studies were limited to nearly or already mature fruits though some studies implied the possibility of seed predator succession during seed development of dipterocarps (Kokubo 1987, Nakagawa *et al.* 2005, Toy 1988). The abortion of damaged fruits occurs before maturation in many plant species (Stephenson 1981), thus sequential sampling throughout seed development is definitely needed. The host range of seed predators is a key to understanding their likely impact on tropical plant

diversity (Lewis & Gripenberg 2008). Particularly, in the case of dipterocarp predators, predator satiation would work in the synchronized fruiting by congeners if they share important predators (Silvertown 1980).

In the present study, we examine the composition of pre-dispersal seed-predator insects on 11 *Shorea* species (Dipterocarpaceae) and some dipterocarp species in other genera in Peninsular Malaysia by sequential seed sampling to test the following hypotheses: (1) a succession of predator species occurs during seed development; (2) dipterocarp species share the same seed predators.

MATERIALS AND METHODS

Study site and tree species examined

The field work was conducted at the permanent 50-ha plot in Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia (2°59′N, 102°18′E and 75–150 m asl). The reserve covers 2450 ha of lowland dipterocarp forest, which is dominated by species of *Shorea* and *Dipterocarpus*. Of the 13 *Shorea* spp. known in the plot, 11 species belonging to six sections were examined (Table 1). Although two relatively rare species – *S. ochrophloia* Strugnell *ex* Sym. and *S. guiso* (Blanco) Bl. – were not included, examined species represented the *Shorea* community in Pasoh well in terms of abundance, comprising 97.5% of total stems of *Shorea* spp. that exceeded 10 cm in dbh in the plot (Kochummen 1997). Three common *Dipterocarpus* spp. and *Neobalanocarpus heimii* (King) Ashton (Dipterocarpaceae) were also examined to compare the species composition of seed predators with those of *Shorea*.

Two consecutive mass-flowering events were used for sampling of seed predators. One occurred from late August 2001 to February 2002 (F-01), and the other occurred from April 2002 to September 2002 (F-02). Since each event had a clear flowering peak and few dipterocarps flowered for several weeks between two events, we treat these events separately in the present study. Detailed information on these flowering events is available in Numata *et al.* (2003) and Sun *et al.* (2007).

Sequential fruit sampling and insect rearing

The fruits used for rearing insects were collected from the ground by hand. Newly fallen fruits were randomly sampled at up to 50 fruits from under each target tree every week during the fruiting events: for 16 wk from November 2001 to February 2002 in F-01 and for 21 wk from April 2002 to September 2002 in F-02. Soon after collection, 50 fruits per tree had their wings cut off, their fresh weight measured and were then stored

Table 1. Tree species and the number of trees and seeds examined, and the maximum weekly mean weight of fresh fruits (without wings). No weight is given for the species that did not bear mature fruit.

Event	Species	Section	Code	N of trees	N of seeds	Maximum weight (mg)
2001	*Shorea acuminata* Dyer	Mutica	ACU1	9	4046	379
	Shorea dasyphylla Foxw.	Mutica	DAS1	1	27	–
	Shorea leprosula Miq.	Mutica	LEPR1	7	2644	610
	Shorea macroptera Dyer	Mutica	MAC1	8	1393	1395
	Shorea parvifolia Dyer	Mutica	PAR1	12	5001	491
	Shorea pauciflora King	Brachypterae	PAU1	4	928	2500
	Shorea bracteolata Dyer	Anthoshorea	BRA1	2	123	1153
2002	*Shorea acuminata* Dyer	Mutica	ACU2	6	1914	381
	Shorea lepidota (Korth.) Bl.	Mutica	LEPI2	6	1480	2111
	Shorea leprosula Miq.	Mutica	LEPR2	6	2187	687
	Shorea macroptera Dyer	Mutica	MAC2	9	3130	1307
	Shorea pauciflora King	Brachypterae	PAU2	5	1397	2402
	Shorea ovalis (Korth.) Bl.	Ovalis	OVA2	3	243	1206
	Shorea maxwelliana King	Shorea	MAX2	6	2039	343
	Shorea hopeifolia (Heim) Sym.	Richetioides	HOP2	1	202	702
	Shorea bracteolata Dyer	Anthoshorea	BRA2	5	156	–
	Dipterocarpus crinitus Dyer		DCI		150	1085
	Dipterocarpus cornutus Dyer		DCR		134	10237
	Dipterocarpus costulatus V. Sl.		DCS		6	–
	Neobalanocarpus heimii (King) Ashton		NHE		283	6620

in 10 plastic boxes ($\leq$5 fruits per box). The insect rearing was conducted for at least 4 mo with appropriate moisture at the laboratory near Pasoh. Emerging adult insects were collected and identified. The host species and the date of seed sampling and insect collecting were recorded together. Our methodology inevitably missed the predators leaving fruits before the fruits dropped. However, the fruits which had an exit hole when sampled were few, suggesting that the majority of insect predators emerged after dispersal.

Comparison in predator frequency between immature and mature seeds

The seed-fall period was divided into three phases based on the relative weight of dropped fruits. The first phase is defined as the period when the mean weight of sampled fruits in a week was 0–15% of its maximum and named 'aborted phase'. Similarly, the second phase and the third phase is the period when the relative fruit weight was 15–60% and 60–100%, respectively. Since fruits were still immature with bright red or light green wings at the second phase while nearly mature to mature with ochre or brown wings at the third phase, we named the second phase 'immature phase' and the third phase 'mature phase'.

The emergence frequency of insects (the number of individuals divided by the number of seeds sampled in each phase) was compared between immature and mature phase by Fisher's exact test for four and five host species

with sufficient number of sampled seeds in F-01 and in F-02, respectively. No comparison was made with the aborted phase, since few adult insects emerged at that phase (Figure 2).

Measurement of host specificity level for predators

The level of host specificity of predator species with more than one individual obtained was measured by the Kullback–Leibler distance (or Kullback–Leibler divergence: d_i) derived from Shannon entropy (Blüthgen *et al.* 2006), which is denoted as

$$d_i = \sum_{j=1} p'_{ij} \ln p'_{ij} / q_j$$

$$p'_{ij} = a_{ij} / \sum_{j=1} a_{ij}, \quad q_j = \sum_{i=1} a_{ij} / \sum_{i=1} \sum_{j=1} a_{ij}$$

where, a_{ij} is the number of insect i from host j. The index considers not only the diversity of hosts but also respective host availability (e.g. the number of sample seeds) (Blüthgen *et al.* 2006), and is standardized as

$$d'_i = (d_i - d_{min})/(d_{max} - d_{min})$$

where, d_{min} and d_{max} is the theoretical minimum and maximum of d_i. This standardized Kullback–Leibler distance (d'_i) ranges from 0 for the most generalized to 1.0 for the most specialized case. Calculation of the index was performed by online Monte Carlo statistics on R $\times$ C matrices (http://itb.biologie.hu-berlin.de/~nils/stat/).

Similarities of seed predator composition among *Shorea* trees

In order to examine the similarity/dissimilarity of predator composition among hosts, an ordination, Detrended Correspondence Analysis (DCA) was carried based on the frequency of predators. The frequency was expressed as the number of emerging individuals from 100 seeds in immature phase and mature phase (excluding abortion phase) for each predator. The predators other than the five abundant species were combined as 'others'. Thus, there were six variables on insect frequency for each host species. The data were square-root transformed prior to the analysis.

The host species that fruited in both events were analysed independently. Three *Dipterocarpus* species were excluded from the analysis since no predators overlapped with those of *Shorea*. *Shorea bracteolata* in F-02 was also excluded since no mature fruits were sampled in the event. A program package PC-ORD ver.4.0 (MJM Software, Gleneden, USA) was used for the DCA.

RESULTS

Species composition of pre-dispersal seed predators

In total, 5211 insects were obtained from 14 162 fruits of the *Shorea* species in F-01 (Appendix 1), and 3166 insects were obtained from 12 748 fruits in F-02 (Appendix 2). Among these, 2144 individuals in F-01 and 1655 individuals in F-02 were weevils or moths, both of which were considered pre-dispersal seed predators. The other insects were hymenopteran parasitoids (Braconidae and Ichneumonidae), orthopteran nymphs, flies (Diptera) and bark beetles (Scolytidae). The flies and bark beetles were not regarded as pre-dispersal seed predators in this study because they were seldom found in fresh fruits. They were probably post-dispersal seed predators or scavengers (bark beetles even sometimes fed on wetted paper used to maintain humidity in the rearing boxes), although the numbers of individuals were sometimes high even in a single fruit. In the present paper, we refer to 'seed predator' or 'predator' only when referring to the pre-dispersal seed predator, i.e. weevils and moths.

Among the predators, two nanophyid weevils: *Nanophyes shoreae* Marshall (Coleoptera: Nanophyidae) (1075 and 1278 individuals in F-01 and F-02, respectively) and Nanophyidae gen. & sp. indet. 1 (nanophyid sp. 1) (209 and 138) and two *Alcidodes* weevils: *A. dipterocarpi* Marshall (Coleoptera: Curculionidae) (245 and 53) and *A. humeralis* Heller (367 and 36), and one moth *Andrioplecta shoreae* Komai (Lepidoptera: Tortricidae) (134 and 93) were dominant in terms of the number of individuals; they comprised more than 80% of all predators in each host except *S.*

bracteolata in F-01 and *S. hopeifolia* in F-02 (Figure 1a), and accounted for 95.5% and 97.0% of all predators.

Neobalanocarpus heimii also hosted nanophyid sp. 1 and *Andrioplecta shoreae*, as well as unique clearwing moth *Synanthedon nautica* Meyrick (Figure 1b). None of the seed predators of *Shorea* spp. emerged from the three *Dipterocarpus* spp., but other weevils of the genus *Damnux* (Nanophyidae) and two pyraustine moth species (Pyralidae) were obtained.

The predator species composition differed significantly between two events in all the five hosts that fruited in both events (Fisher's exact test, $P < 0.001$ for *S. acuminata*, *S. leprosula* and *S. macroptera*, $P = 0.038$ for *S. pauciflora*) except *S. bracteolata* ($P = 0.467$) (Figure 1a). The relative abundance of *N. shoreae* to the total predators was significantly larger in F-02 than F-01 in *S. leprosula* and *S. macroptera* (Fisher's exact test, $P < 0.001$), and this was true for that of nanophyid sp. 1 in *S. acuminata* ($P < 0.001$). By contrast, that of *Alcidodes dipterocarpi* and *A. humeralis* was significantly smaller in F-02 than F-01 ($P < 0.001$) in *S. acuminata*, *S. leprosula* and *S. macroptera*. *Andrioplecta shoreae* was also significantly more abundant in F-01 than F-02 in *S. acuminata* ($P < 0.001$) and *S. leprosula* ($P < 0.05$).

Temporal pattern of predator species composition during seed development

The predator species composition changed over the seed developmental period. For example, *Shorea acuminata* in F-01 (Figure 2), the nanophyid spp. began to emerge from fruits dropped 7 wk after flowering and continued to emerge for another 7 wk. On the other hand, *Alcidodes* spp. started to emerge from fruits dropped 10 wk after flowering and continued until just before the end of seed fall. The frequency of nanophyid spp. was significantly higher during the immature phase than the mature phase (Fisher's exact test, $P < 0.001$) while that of *Alcidodes* spp. was significantly higher in the mature phase than the immature phase ($P < 0.001$). The predator species succession during seed development occurred in the same way in other hosts (Table 2). *Andrioplecta shoreae* was also found significantly more frequently in the mature phase than the immature phase for some hosts ($P < 0.05$) (Table 2). However, this species seemed to feed on seeds (or fruits) of various stages and its larvae were often observed even earlier than those of nanophyid spp.

The level of host specificity of predators

The degree of host specificity (d') ranged from 0.03 to 0.94 among predator species, with the weighted average of 0.16 and 0.20 in F-01 and F-02, respectively. Most predator species were below the average in host specificity in both events (Figure 3). As for the five abundant
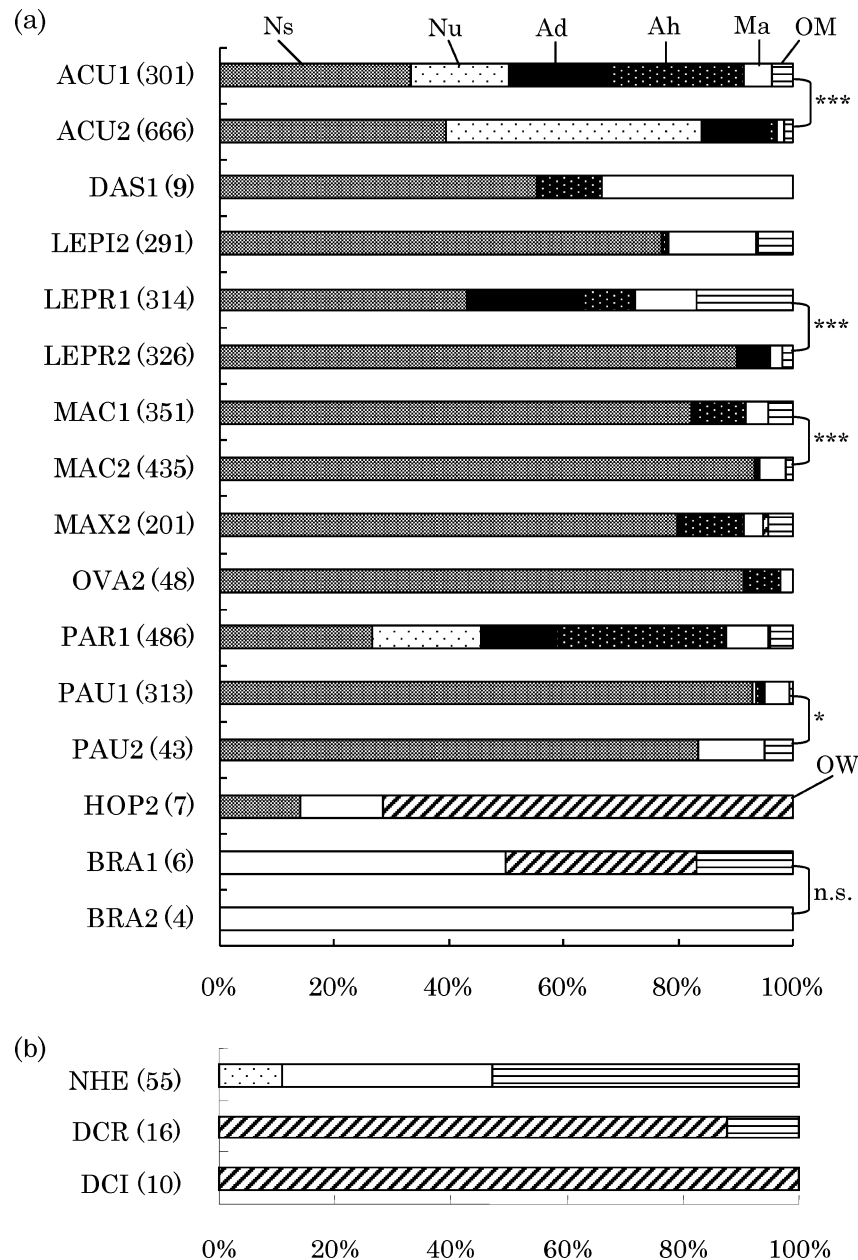
Figure 1. The composition of individual numbers of seed predatory insects emerged from seeds of *Shorea* species (a) and from seeds of other genera (b). The total number of seed predators is shown in the parentheses following the code name of hosts. No data for *Dipterocarpus costulatus* is presented here since only one individual weevil was obtained from the host (Appendix 2). * P < 0.05, *** P < 0.001 (Fisher's exact test). Ns: *Nanophyes shoreae*, Nu: nanophyid sp. 1, Ad: *Alcidodes dipterocarpi*, Ah: *A. humeralis*, Ma: *Andrioplecta shoreae*: OW: other weevils, OM: other moths. See Table 1 for the code names of the hosts.

predators, *Andrioplecta shoreae* showed the lowest d' of the five. The host specificity of *N. shoreae*, *Alcidodes dipterocarpi* and *A. humeralis* were around the average, and nanophyid sp. 1 was higher than the average in both events. No correlation was found between d' and relative abundance (Spearman's rank correlation, n = 14, r = −0.07, P = 0.982 in F-01; n = 11, r = 0.141, P = 0.679 in F-02). The average of d' was higher in F-02 than F-01 and it was true for all the five abundant predators except *N. shoreae*.

Similarity of seed predator composition among *Shorea* species

The Axis 1 and Axis 2 extracted by DCA based on the abundance of predators explained 56.2% and 10.3% of the total variance, respectively (Figure 4). Axis 1 was correlated with the frequency of *N. shoreae* negatively (r = −0.911) and with 'others' positively (r = 0.855). Axis 2 was correlated with the frequency of *Andrioplecta shoreae* negatively (r = −0.242) and with nanophyid

Table 2. The result of comparison in predator frequency between immature and mature phase for six host species in two fruiting events. The code name for insect species is shown in the column in which phase it emerged significantly more frequently. ns = no significant difference between phases. The comparison in frequency was made by Fisher's exact test (*P < 0.05, **P < 0.01, ***P < 0.001). Ns: *Nanophyes shoreae*, Nu: nanophyid sp. 1, Ad: *Alcidodes dipterocarpi*, Ah: *A. humeralis*, Ma: *Andrioplecta shoreae*.

Host Species	Event	Immature phase	Mature phase	ns
Shorea acuminata	F-01	Ns, Nu***	Ad, Ah***; Ma*	
	F-02	Ns, Nu***	Ad***	Ah, Ma
S. lepidota	F-02	Ns***		Ma
S. leprosula	F-01	Ns***	Ad, Ah***; Ma**	
	F-02	Ns***		Ad, Ah, Ma
S. macroptera	F-01	Ns***	Ad, Ah***	Ma
	F-02	Ns***	Ad, Ma***	
S. maxwelliana	F-02	Ns***	Ah***	Ma
S. parvifolia	F-01	Ns, Nu***	Ad, Ah***; Ma*	

sp. 1 (r = 0.892) and *Alcidodes dipterocarpi* (r = 0.835) positively.

Many of the *Shorea* species were clumped in the lower scores of Axis 1 due to the dominance of *N. shoreae* (Figure 4, Group 1). However, *S. acuminata* and *S. parvifolia* were outstanding in higher scores of Axis 2 since they had nanophyid sp. 1 and *Alcidodes dipterocarpi* abundantly as well as *Nanophyes shoreae* (Group 2). *Shorea hopeifolia*, *S. bracteolata* and *Neobalanocarpus heimii* had higher scores in Axis 1 since they had little or no *N. shoreae* but more 'others' (Group 3). The same tree species of different events were in the same group, suggesting that abundant predator species did not differ largely within the same host between events.

DISCUSSION

Pre-dispersal seed predator composition

In the present study, we found four weevil species: *Nanophyes shoreae*, nanophyid sp. 1, *Alcidodes dipterocarpi* and *A. humeralis*, and one moth species *Andrioplecta shoreae* were abundant on *Shorea* seeds. Principally, an individual larva of the predators feeds and kills one individual seed, thus dominance of these predators indicates their importance in terms of the number of seeds destroyed. *Shorea* species examined in the present study are typical and widely distributed throughout lowland rain forests of Peninsular Malaysia. Thus, the
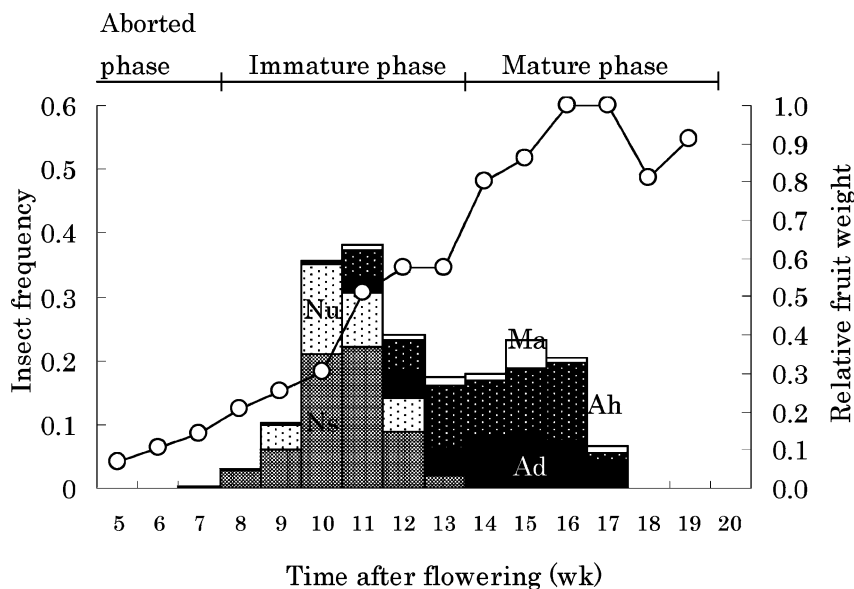

Figure 2. Temporal patterns of insect predator frequency in dropped fruits (bar) and relative fruit weight (circle) during seed developmental period of *Shorea acuminata* in F-01. Fruiting period was divided into three phases based on the relative fruit weight. Ns: *Nanophyes shoreae*, Nu: nanophyid sp. 1, Ad: *Alcidodes dipterocarpi*, Ah: *A. humeralis*, Ma: *Andrioplecta shoreae*: OW: other weevils, OM: other moths.
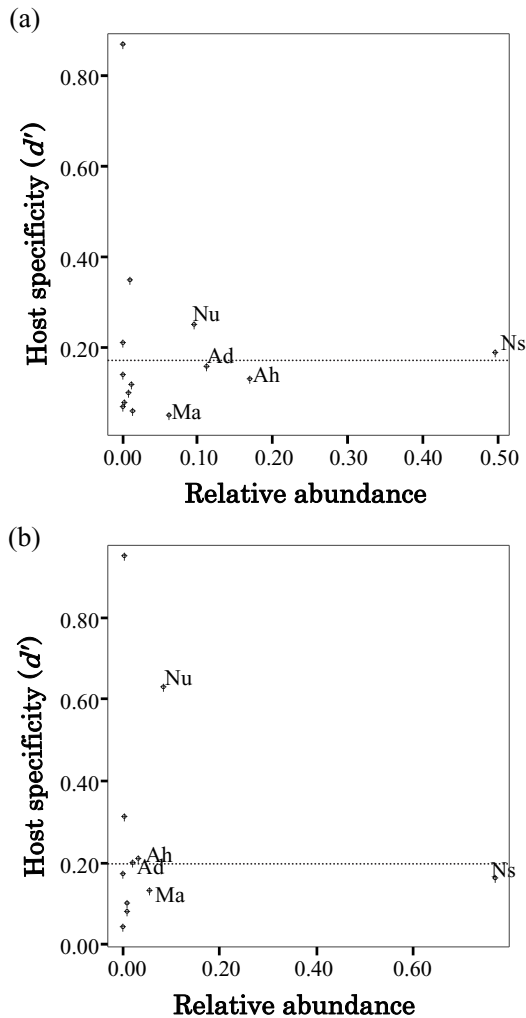
(a)

(b)

Figure 3. Relative abundance (all *Shorea* combined) and the degree of host specificity measured by standardized Kullback–Leibler distance (d') of insect predators (N ≥ 2) in F-01 (a) and F-02 (b). The five abundant predators are indicated as follows, Ns: *Nanophyes shoreae*, Nu: nanophyid sp. 1, Ad: *Alcidodes dipterocarpi*, Ah: *A. humeralis*, Ma: *Andrioplecta shoreae*.

Figure 4. Ordination of host species by DCA based on the abundance of each predator species (number of predators per seed). See Table 1 for the code names of the hosts.

might be more suitable for consecutive fruiting events like F-01 and F-02 than other predator species.

Species succession of seed predators during seed development

The sequential sampling over seed development revealed many seeds were attacked and aborted before seed maturation. Predator species changed considerably during the seed developmental period; the nanophyid weevils were found in immature aborted seeds while *Alcidodes* weevils were found in nearly mature to mature dropped seeds (Figure 2). Species succession of insect predators during seed development has been reported in other plants (Fukumoto & Kajimura 2001, Igarashi & Kamata 1997). Fukumoto & Kajimura (2001) successfully categorized insect seed predators of Japanese oaks into three guilds: pistillate-flower-feeding guild, immature-acorn-feeding guild, and mature-acorn-feeding guild. They bagged canopy twigs with fruits sequentially during seed development in order to determine oviposition period of insects. The nanophyid weevils, *Alcidodes* weevils and *Andrioplecta shoreae* in the present study probably correspond to immature seed-feeding, mature (or nearly mature) seed-feeding, and all seed-feeding predators, respectively, based on the information when they aborted. The oviposition timing of dipterocarp predators has not been revealed except that of *N. shoreae*, which oviposit within 15–48 d after peak anthesis (Toy 1991). It is essential to determine the oviposition period for other predators to fully understand the timing of predation.

In dipterocarps, most initiated fruits, whether damaged or undamaged, are known to be aborted before

dominance of these predators on *Shorea* seeds is likely to be common in that region. On the other hand, Nakagawa *et al.* (2003) reported from Borneo that weevils in the genera *Orchestes* (Curculionidae) or *Aracerus* (Anthribidae) were also abundant as well as *Nanophyes* and *Alcidodes* (*Sternuchopsis* in their paper) in *Shorea* seeds. Reflecting the higher number of *Shorea* species in Borneo: 138 *Shorea* in Borneo (Ashton 2004) and 58 in Peninsular Malaysia (Symington 2004), seed predator weevils might be more diverse in Borneo than Peninsular Malaysia.

The year-to-year variation in relative abundance of seed predators indicated that *N. shoreae* and nanophyid sp. 1 were proportionately more abundant in F-02 than F-01 (Figure 1). Their biology, e.g. reproductive cycle,
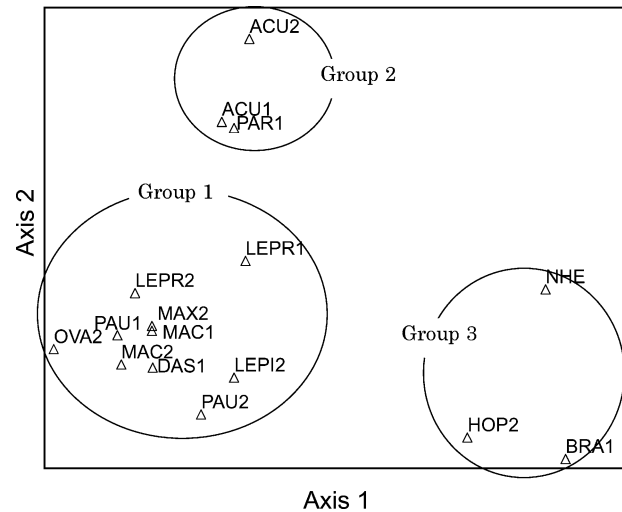
maturation (Momose *et al.* 1996, Naito 2008, Nakagawa *et al.* 2005, Sakai *et al.* 1999). Only a small proportion of initiated fruit can grow with sufficient resources provided by the mother tree. Momose *et al.* (1996) observed that only 3.6% of the total number of flowers received 47% of the total reproductive investment in dry weight and matured to germination. In this context, loss of resource and reduction of sound seed production due to predation, would differ considerably with the timing of predation, i.e. the greater impact on sound seed production occurs during late predation. Immature seed predation by nanophyid spp. was observed more frequently than that by other predators, but the fruit loss due to this predation might be compensated for by undamaged fruits that would otherwise be aborted later. Insect exclusion did not affect the seed survivorship at the earlier stages of seed development of *Dryobalanops aromatica* while it did affect negatively at the later stage (Nakagawa *et al.* 2005). Therefore, predation by *Alcidodes* spp., rather than by nanophyid spp., might cause greater resource loss and reduce the total number of sound seeds produced.

Host specificity of predators

The degree of host specificity (d') of most predator species was below the low average (0.16 in F-01 and 0.20 in F-02) (Figure 3), suggesting that insect predators have low host specificity to *Shorea* seeds. The exceptions were *Alcidodes* sp. 1 ($d_i' = 0.86$) in F-01 and *A. shoreaphilus* (0.94) in F-02, which emerged only from *S. bracteolata* and *S. hopeifolia*, respectively. Among the five abundant predators, nanophyid sp. 1 showed higher host specificity than others. The weevil mostly emerged from *S. acuminata* or *S. parvifolia*, even though it had at least six *Shorea* hosts (Appendices 1 and 2), suggesting its strong preference to these hosts. When *S. parvifolia* did not fruit well in F-02, the weevils aggregated to *S. acuminata* ($d' = 0.62$).

Since the fruiting frequency is different even among closely related *Shorea* species (Numata *et al.* 2001), the species composition of fruiting trees is often different between fruiting events (Brearley *et al.* 2007). The low host specificity would be advantageous to the predators to maximize the opportunity for utilizing fruiting events.

Similarity of seed predator composition among *Shorea* species

With the dominance of *N. shoreae*, the scores in DCA Axis 1 were low for many *Shorea* species in Pasoh (Figure 4, Groups 1 and 2). Host species in group 1 shared three of the five abundant predators: *N. shoreae*, *Alcidodes humeralis* and *Andrioplecta shorae* while those in group 2,

S. acuminata and *S. parvifolia*, had all of the five abundant predators (Figure 2). The hosts in group 3 had only one or two of the five abundant predators but often had unique ones, e.g. *Alcidodes shoreaphilus* Lyal from *S. hopeifolia* or *A.* sp. 1 from *S. bracteolata* (Appendices 1 and 2).

All trees in group 1 and 2 belong to a timber group Red Meranti which consists of sections *Mutica*, *Brachypterae* and *Ovalis*, except *S. maxwelliana* (section *Shorea*) belonging to a timber group Balau. On the other hand, *S. hopeifolia* (section *Richetioides*) and *S. bracteolata* (section *Anthoshorea*) in group 3 belong to a timber group Yellow Meranti and White Meranti, respectively. Kamiya *et al.* (2005) reported nuclear gene *PgiC* of Red Meranti was closely related to Balau, and they were closer to Yellow Meranti than White Meranti. Furthermore, White Meranti is very close to *Neobalanocarpus.* This is roughly consistent with the scores of DCA Axis 1 (Figure 4), thus differences in compositions of insect seed predators may well reflect the phylogenetic distance between sections or timber groups of the hosts.

Implications for predator satiation of insect predators

Silvertown (1980) pointed out three interdependent elements for predator satiation to work: (1) production of enough seeds to satiate predators, (2) sufficient interval between fruiting events to reduce the population of predators, (3) sharing the same seed predators among sympatric species fruiting synchronously. Wide overlap of seed predators among many *Shorea* spp. in Pasoh ensures the third element. Synchronized mast seeding by congeneric trees sharing the same seed predators has been reported in *Chionochloa* spp. (Poaceae) from New Zealand (Kelly *et al.* 2000, McKone *et al.* 2001) and the cycad *Encephalartos* spp. from South Africa (Donaldson 1993).

On the other hand, there were two findings that might contradict the second element. First, predators probably have alternative hosts that are available between mast fruiting years. For example, nanophyid sp. 1 and *Andrioplecta shoreae* were also obtained from *Neobalanocarpus heimii* in the present study (Figure 1b). Unlike other dipterocarps, *N. heimii* is known to fruit almost every year at the population level (Burgess 1972, Marzalina *et al.* 2003). Furthermore it takes 6 mo to grow seeds and another 1 y to complete seed dispersal (M. Yasuda, pers. comm.). One can thus find its fruits in various developmental stages at almost any time of the year (Hosaka *et al.* 2007). Therefore, the two insect species certainly rely on *N. heimii* during the non-fruiting period of *Shorea* trees, the second most abundant dipterocarp species in our plot (Kochummen 1997). Nakagawa *et al.* (2003) found some of the dipterocarp seed predators including *Nanophyes shoreae*, *Alcidodes dipterocarpi* and

Andrioplecta shoreae, from trees of other families such as Moraceae, Myrtaceae, Celastraceae and Sapotaceae. The rather wide host range of these insects might enable them to reproduce and keep their populations between mast-fruiting events.

Second, weevil predators might have an extended diapause. We found many weevil larvae still alive and probably in diapause after 4-mo rearing. Some of the larvae lived more than 1 y in the rearing boxes. A similar observation was reported by Nakagawa *et al.* (2003). The extended diapause is known in many seed predators both in larval and adult stages (Donaldson 1993, Hanski 1988, Janzen 1971, Kelly *et al.* 2000, Maeto & Ozaki 2003), and might be effective to track years of masting by responding to the same weather cue as the plants (Kelly *et al.* 2000).

However, it should be noted that, although seeds of *N. heimii* are available throughout the year, its density was not comparable to that of *Shorea* spp. in mast years. In addition, since carnivorous animals and disease micro-organisms are active throughout the year in the aseasonal tropics, mortality is likely to be high during years of diapause. Thus, population size of predators would become smaller after a mast fruiting event even they have alternative hosts and/or diapause. Moreover, Kelly *et al.* (2000) argued that such counter-adaptations of predators might even contribute to maintaining or strengthening the selection for extreme masting, since predators would become harder to satiate by normal levels of masting.

It is difficult to explain fruiting synchrony at family level by satiation of pre-dispersal insect seed predators alone since no predator overlap was found between *Shorea* and *Dipterocarpus* in the present study, in contrast to the results from Borneo (Nakagawa *et al.* 2003). The original idea of predator satiation in the mast fruiting of dipterocarps assumed polyphagous post-dispersal vertebrate predators (Janzen 1974), and some evidence to support the idea has been presented (Curran & Leighton 2000, Curran & Webb 2000). However, considering the wide overlap of important insect predators among *Shorea*, the synchronized mast fruiting by congenerics is possibly also effective for avoiding pre-dispersal seed predators. Thus it would be important in order to produce and disperse a large number of viable seeds sufficient for swamping post-dispersal predators.

ACKNOWLEDGEMENTS

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Appendix 1. A list of insects that emerged from dipterocarp fruits in 2001 flowering. The codes for plant species are as follows. AC: *Shorea acuminata*, BR: *S. bracteolata*, DS: *S. dasyphylla*, LR: *S. leprosula*, MC: *S. macroptera*, PR: *S. parvifolia*, PU: *S. pauciflora*.

	Tree species							
	AC	BR	DS	LR	MC	PR	PU	Total *Shorea*
Number of seeds	4046	123	27	2644	1393	5001	928	14162
Weevils (Coleoptera)								
Nanophyes shoreae Marshall (Nanophyidae)	224		5	136	289	130	291	1075
Nanophyidae sp. 1 (Nanophyidae)	114			1		91	2	117
Alcidodes dipterocarpi Marshall (Curculionidae)	117			60	4	64		245
Alcidodes humeralis Heller (Curculionidae)	156		1	31	30	144	5	367
Alcidodes sp. 1 (Curculionidae)		2						2
Curculio sp. (Curculionidae)						1		1
Rhynchitidae sp.	1							1
Moths (Lepidoptera)								
Andrioplecta shoreae Komai (Tortricidae)	31	3	3	34	13	36	14	134
Assara albicostalis Walker (Pyralidae)	13			6	8	4		31
Lamoria adaptella Walker (Pyralidae)				2				2
Stathmopodinae sp. 1 (Oecophoridae)	2	1		19				22
Stathmopodinae sp. 2 (Oecophoridae)	3			10	1	4	1	19
Hieromantis sp. (Oecophoridae)	3			11	2	10		26
Other Lepidoptera	2			4	4	1		11
Barkbeetles (Coleoptera: Scolytidae)	65		36	678	906	549	398	2632
Other beetles (Coleoptera)	3	2	1	12	13	24	6	61
Flies (Diptera)	15	46	2	38	9	36	23	169
Parasitoid wasps (Hymenoptera: Braconidae and Ichneumonidae)	37	3		25	14	19	27	125
Tree hoppers (Orthoptera)	3			13	2	10	52	80

Appendix 2. A list of insects that emerged from dipterocarp fruits in the 2002 flowering. HP: *S. hopeifolia*, LI: *S. lepidota*, MX: *S. maxwelliana*, OV: *S. ovalis*, DI: *Dipterocarpus crinitus*, DR: *D. cornutus*, DS: *D. costulatus*, NH: *Neobalanocarpus heimii*.

	AC	BR	HP	LI	LR	MC	MX	OV	PU	Total *Shorea*	DI	DO	DS	NH
Number of seeds	1914	156	202	2187	1480	3130	2039	243	1397	12748	150	134	6	283[1]
Weevils (Coleoptera)														
Nanophyes shoreae (Nanophyidae)	119		1	224	295	407	161	44	36	656				
Nanophyidae sp. 1 (Nanophyidae)	134			1	1	1				3				6
Nanophyidae sp. 2 (Nanophyidae)							1			1				
Nanophyidae sp. 3				1						1				
Damnux tindaleorum Lyal (Nanophyidae)										0		3	1	
Damnux tenebriosa Lyal (Nanophyidae)										0		8		
Damnux cf. *conviva* Lyal (Nanophyidae)										0	4			
Damnux sp. 1 (Nanophyidae)										0		1		
Damnux sp. 2 (Nanophyidae)										0	2			
Alcidodes caviventris Lyal (Curculionidae)							1			1				
Alcidodes dipterocarpi (Curculionidae)	33				15	3	2			53				
Alcidodes humeralis (Curculionidae)	6			2	3	1	21	3		36				
Alcidodes shoreaphilus Lyal (Curculionidae)			5							5				
Moths (Lepidoptera)														
Andrioplecta shoreae (Tortricidae)	4	4	1	45	7	19	7	1	5	93				20
Assara albicostalis (Pyralidae)	1									1				7
Lamoria adaptella (Pyralidae)														2
Stathmopodinae sp. 1 (Oecophoridae)				1	1					2				
Stathmopodinae sp. 2 (Oecophoridae)	1			8	3	2	1			15				
Hieromantis sp. (Oecophoridae)	2			6		3	5			16				10
Synanthedon nautica Meyrick (Sesiidae)														10
Pyralidae sp.1										0		1		
Pyralidae sp.2										0		1		
Other Lepidoptera				2	1		2		2	7				5
Barkbeetles (Coleoptera: Scolytidae)	21	1	46	642	63	257	41	97	70	1238	28	48		134
Other beetles (Coleoptera)				2		1			2	5				
Flies (Diptera)	6			10		6	1			23		8		
Parasitoid wasps (Hymenoptera: Braconidae and Ichneumonidae)	40	5		34	12	6	9	1	6	113	8			
Tree hoppers (Orthoptera)			1	115	2				14	132		1		6

[1] Including fruits originally from the 2001 flowering.