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Insect assemblages attacking seeds and fruits in a rainforest in Thailand

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Abstract

Insect seed predators are important agents of mortality for tropical trees, but little is known about the impact of these herbivores in rainforests. During three years at Khao Chong (KHC) in southern Thailand we reared 17,555 insects from 343.2 kg or 39,252 seeds/fruits representing 357 liana and tree species. A commented list of the 243 insect species identified is provided, with details about their host plants. We observed that: (1) about 43% of identified species can be considered pests. Most were seed eaters, particularly on dry fruits. (2) About 19% of parasitoid species (all Opiinae) for which we could determine whether their primary insect host was a pest or not (all Bactrocera spp. breeding in fruits) can be considered beneficials. (3) The seeds/fruits of about 28% of the plant species in this forest were free of attack. Phyllanthaceae, Rubiaceae, and Meliaceae were attacked relatively infrequently; in contrast, Annonaceae, Fabaceae, Sapindaceae, and Myristicaceae were more heavily attacked. There was no apparent effect of plant phylogeny on rates of attack but heavily attacked tree species had larger basal area in the KHC plot than rarely attacked tree species. (4) Insects reared from fleshy fruits were more likely to exhibit relatively stable populations compared to insects reared from dry fruits, but this was not true of insects reared from dipterocarps, which appeared to have relatively stable populations throughout the study period. We tentatively conclude that insects feeding on seeds and fruits have little effect on observed levels of host abundance in this forest.

Key words: dipterocarp, parasitoid, pest, seed predation, Tephritidae.

INTRODUCTION

Insect seed predators represent important agents of mortality for tropical rainforest trees because they often kill the plant embryo, or make the fruit unsuitable for seed dispersers (Janzen 1970; Lewis & Gripenberg 2008). Insects feeding internally on fleshy fruits can also cause significant loss of plant fitness and economic damage, via, notably, fruit abortion (Stephenson 1981). There is an abundant literature on seed predators as pests of economic plants (e.g. Zehnder *et al*. 2007) or on seed- and fruit-feeding insects in temperate areas (e.g. Turgeon *et al*. 1994) but in comparison little is known about these in tropical rainforests where community-level studies of insects feeding on seeds (dry fruits, achenes) and fleshy fruits are extremely rare. This is because it is difficult to survey the extremely diverse range of potential host plants with adequate spatial and temporal sampling effort, particularly with regard to pre-dispersal seed predation (Ctvrtecka *et al*. 2014). To the best of our knowledge, there are currently only six such examples which are relatively comprehensive. (1) Janzen studies of insect seed predation in Guanacaste (targeting beetles and summarized in Janzen 1971) led to the formulation of the Janzen-Connell hypothesis, explaining the coexistence of tree species in tropical forests as resulting from negative density-dependence processes (Janzen 1970). (2) Nakagawa, Hosaka and their colleagues have studied insect seed predation in dipterocarp forests at two locations in Malaysia (Nakagawa *et al*. 2003, 2005; Hosaka *et al*. 2009, 2011; Iku *et al*., 2017). (3) Copeland *et al*. (2009) made a broad survey of insects feeding on wild fruits in Kenya, targeting tephritids. (4) Ramírez and Traveset (2010) published a comprehensive survey of insect seed predators in different habitats in Venezuela, including discontinuous patches of forest. (5) Ctvrtecka and colleagues studied insects feeding on both seeds and fruits with high sampling effort in a lowland forest of Papua New Guinea (Ctvrtecka *et al*. 2014, 2016; Sam *et al*. 2017). (6) More recently, Gripenberg *et al*. (2018, unpubl. data) conducted a similar survey on Barro Colorado Island in Panama.

The present contribution adds the first study in Thailand. We have summarized the higher faunal composition of the insects reared from seeds and fruits at this location

(Basset *et al*. 2018) and intend to discuss interaction networks in detail elsewhere. In this contribution, we attempt to answer various questions related to three general hypotheses that are particularly relevant to the identity *per se* of the plants surveyed and insect species reared.

First, forests may act as reservoirs of both fruit/seed-feeding pests and their parasitoids. For example, most research on frugivorous insects from wild fruit is specifically concerned with discovering the range of reservoir hosts of fruit flies (Tephritidae), which are major pests of commercial fruit crops (Allwood *et al*. 1999; Copeland *et al*. 2009). Given that most insect herbivores in tropical rainforests are reasonably host-specific (Novotny *et al*. 2002), it is not immediately clear whether a relatively pristine forest may contribute significantly as a reservoir of pests of cultivated plants, or of potential parasitoids of such pests. Further, forest pests attacking the seeds of ecologically and economically important species of timber trees, such as many species of Dipterocarpaceae (Lyal & Curran 2000), may spread into plantations of these species. The forest may also potentially act as a reservoir of pests of stored products because these insects usually feed on a resource low in water (Subramanyam 1995), similar to that of seed predators of dry fruits (achenes; Janzen 1980). Rainforests might also act as reservoirs of beneficial insects, such as parasitoids of pest species (Aluja *et al*. 2014). The enemy hypothesis states that predatory insects and parasitoids are more effective at controlling populations of herbivores in diverse systems of vegetation than in simple ones (Russell 1989). For example, there is evidence that diverse wet and dry forests in Mexico and Central America act as reservoirs of parasitoids attacking fruit flies in fruit orchards. This mechanism contributes to the value of tropical tree conservation in Mexico (Aluja *et al*. 2014).

Second, the identity of the plants and insects involved in interactions is crucial for two reasons. The identity of plants whose levels of seed/fruit attack stand out from the rest of the local vegetation (i.e. rarely or heavily attacked) is important because it can shed light on patterns of insect host shifts and use (Janzen 1985) and, ultimately, to practical measures of crop protection. The identity (or absence of) of the enemies of seed eaters, such as insect parasitoids, is also important because some granivores and frugivores may be relatively free of enemies, perhaps suggesting effective defenses. The nasty host hypothesis proposes that insect herbivores feeding on plant hosts with strong and/or distinctive chemical defenses may support a reduced load of parasitoids because their tissues may be more toxic to parasitoids (Gauld *et al*. 1992). Given the potential importance of insect seed predators in tropical tree mortality (Lewis & Gripenberg 2008), this hypothesis may have consequences for the local distribution of tree species and the dynamics of their populations.

Finally, seed predators are thought to be satiated by mass production of seeds, which promotes escape from predation. The satiation hypothesis has been well-studied in dipterocarp forests of Malaysia (Curran & Webb 2000). The whereabouts of seed-predators of mast-fruiting trees, such as dipterocarps in many forests, in-between periods of masting, which can be as long as several years, is crucial for these specialized insects (Hosaka *et al*.

2011). The extent of annual fluctuations of seed predators in tropical rainforests has not been well-studied, with the exception of dipterocarp seed predators, which may maintain populations by prolonged dormancy and/or alternative hosts (Hosaka *et al*. 2011). This issue could help understanding patterns of insect attack on particular plant species, and their local distribution and abundance. Here again the identity of both plants and insects are crucial to evaluate potential patterns.

The general aims of this paper are to document (as far as possible) the identity of insects attacking seeds and fruits, as well as their main parasitoids, in a lowland rainforest in Thailand. Our specific questions are as follows:

1) Does this forest represent a potential reservoir of pests for seed and fruit crops or seeds of valuable timber trees, such as dipterocarps, in Thailand?

2) Does this forest represent a reservoir of parasitoids potentially able to control pests of seeds and fruits in Thailand?

3) Which taxa of seed/fruit-feeding insects are relatively free of parasitoids?

4) Which tree species suffer unusual rates of seed/fruit attack in this forest? Are these tree species particularly rare or abundant in this forest?

5) Which insect species maintain relatively high and stable populations during the study years?

MATERIALS AND METHODS

Study site

Our study site included the 24 ha ForestGEO permanent vegetation plot (https://forestgeo.si.edu/; see below) at Khao Chong (KHC; 7° 32' N, 99° 47' E, altitude 120-330 m) and the surrounding forest (i.e. an area of ca. 1,500 ha). This permanent plot is located in the protected lowland seasonal evergreen forest of the Khao Ban Thad Wildlife Sanctuary in Southern Thailand and is described in detail by Anderson-Teixeira *et al.* (2014). Mean annual rainfall is 2,665 mm and mean daily maximum air temperature is

27.1°C. KHC experiences a 2 to 3 months seasonal drought from January to March (drought defined as any month receiving <100 mm of rainfall: Baltzer & Davies 2012). In the ForestGEO plot, all trees with a diameter at breast height (DBH) of 1 cm or greater have been mapped and identified to species (Anderson-Teixeira *et al*. 2014). There are 593 tree species, representing 285 tree genera and 82 plant families in the plot, with approximately 300 species per ha (Baltzer & Davies 2012). The proportion of plant species with dry fruits (achenes) is 26.0% and total seed rain is 7.0 dry g x m^{-2} x yr^{-1} (Basset *et al*. 2018). Although 13 dipterocarp species grow at KHC (representing 11.8% of stems and 23% of the basal area in the ForestGEO plot; Bunyavejchewin *et al*. 2011), phenological studies demonstrated that the reproductive phenology of the KHC forest was more similar to tropical forests with similar rainfall seasonality in other parts of the world than it was to dipterocarp-dominated forests in ever wet regions of Southeast Asia (Kurten *et al*. 2017).

Survey of plants and rearing of insects

Plant surveying and the rearing of insects from seeds and fruits are detailed in Basset *et al*. (2018). Briefly, in 2013 we surveyed seeds and fruits of locally abundant tree, shrub and liana (more rarely herb) species. During 2014 and 2015, we restricted our sampling effort to 10 plant families, which represented the most common families at KHC. We refer to these families as focal families and they included: Annonaceae, Arecaceae, Ebenaceae, Euphorbiaceae, Fabaceae, Lauraceae, Meliaceae, Phyllanthaceae, Rubiaceae and Sapindaceae. Unless specified, results are detailed for all host plant species. Seeds and fruits collected on plants or freshly fallen (without apparent decomposition) were targeted, thus focusing on pre-dispersal attack (i.e. on insects attacking developing or mature seeds in the canopy of trees). Host plants were identified and their seeds/fruits assigned to the following seed and fruit "syndromes" (hereafter seed syndromes for brevity; see Basset *et al*. 2018 for more details): A1.1, fleshy drupe with thick mesocarp (>5 mm); A1.2, fleshy drupe with thin mesocarp (<5 mm); A2.1, non-fleshy drupe with thick mesocarp (>5 mm);

A2.2, non-fleshy drupe with thin mesocarp (<5 mm); B1, fleshy indehiscent fruit with multiple seeds; B2, non-fleshy dehiscent fruit with multiple seeds; C1, dry winged seed that does not develop in capsule; and C2, multiple dry seeds (with or without wings) that develop in a capsule/pod (opening across one axis). These categories were recombined in some analyses as just 'fleshy fruits' (= A1.1, A1.2, B1) or just 'dry fruits' (achenes= A2.1, A2.2, B2, C1, C2).

Rearing sample units included clusters of conspecific seeds/fruits of similar size collected from the same trees. We targeted as many individuals as possible for each plant species, typically > 5. These sample units were weighed (fresh weight) and stored in individual plastic pots. Pots were lined with tissue paper and covered with very fine netting for ventilation and to avoid subsequent colonization/contamination of fruits by, notably, drosophilid flies (Copeland *et al*. 2009). Rearing pots were stored under semi-natural conditions in covered but ventilated sheds under the forest canopy. They were checked twice weekly, and any emerging insects were collected, preserved, mounted and then identified (see below). Seeds/fruits were stored for 3 months, and then dissected to ensure that there were no developing larvae inside. Seed/fruits with live larvae were reared for longer, while other seeds/fruits were discarded.

Insect identification

The level of identification was unequal among insect orders owing to the availability of specialists on particular insect groups. In general, beetle and moth families were identified mostly to species level, whereas for Diptera and Hymenoptera only Stratiomyidae, Tephritidae and Ichneumonoidea were sorted to species level. We obtained DNA Cytochrome c oxidase subunit I (COI, ‘DNA barcode’) sequences from legs of representative specimens, and we used Barcode Index Numbers (BINs) derived from insect sequences to delineate species (Ratnasingham *et al*. 2013). Unfortunately, most of the original high-quality DNA samples were spoiled in the sequencing laboratory of the Smithsonian Tropical Research Institute, and in the meantime the remaining specimens had been exposed to high humidity, so we were unable to obtain DNA sequences from all species. Data were deposited in the Barcode of Life projects KHCSP and KHCTE (398 sequences). Full specimen data for specimens sequenced (including those that failed), including images and host plants, are available on BOLD (www.boldsystems.org), accessible from the data set KHCFRUIT using a DOI (dx.doi.org/10.5883/DS-KHCFRUIT). Morphological identification of specimens, when possible, was performed by RT, SEM, JWB, DLJQ, MK, PP, MS, and by colleagues cited in the Acknowledgements. For Lepidoptera, nomenclature follows Holloway (2011) and Holloway *et al*. (2001). Insect vouchers are deposited at the Thai Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand, and the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Insects reared from seeds/fruits were assigned to a guild system at the family, subfamily, or in some cases at the generic or specific level (details in Basset *et al*. 2018). Here we only consider three guilds: seed eaters (coded as SE: larva feeding mostly on seed tissue), pulp eaters (PU: larva feeding mostly on mesocarp tissue), and parasitoids (PA: larva feeding on insect hosts). Members of the moth families Blastobasidae and Tineidae, which are predominantly scavengers, were not included in the analyses, but when available, we nevertheless provided basic information about them.

Assessing the pest status of insect species identified is not an easy task. For Lepidoptera, we examined the list of species of economic importance compiled by Zhang (1994). We further considered for pest species the number of citations occurring in the *Review of Applied Entomology* (up to 1994) as an indication of the severity of the pest (Zhang 1994). Additionally, we considered the host records of Kuroko and Lewvanich (1993) for Thailand. For Tephritidae we followed the nomenclature and pest status as indicated in Doorenweerd *et al*. (2018). The pest status of Scolytinae was inferred from Browne (1961) and other sources indicated in Appendix S1, as for the rest of beetles. Finally, we also considered the species listed as pests and beneficial insects in Thailand (Hutacharern & Tubtim 1995).

Regarding the parasitoids, we considered interactions between members of the Braconidae and Icheumonidae (both Ichneumonoidea) and their insect hosts; these two families represented most of the parasitoids that we reared. Unlike with the host plants, our interpretations of the hosts of the reared parasitoids only reflect 'high expectations of interactions', not documented interactions. This is because parasitized hosts were not isolated and reared individually, the parasitoids instead being reared from samples including relatively high numbers of seeds and fruits. To assign putative hosts to each parasitoid species, we applied three simple rules in decreasing number of importance: (1) since many ichneumonoid lineages are rather conservative in host use, we followed Quicke (2015) to select the most likely host order or family; (2) we then examined for each parasitoid species, the co-occurrence of primary consumers in each sample from which this parasitoid species was reared; and finally (3) we considered the highest abundance of putative host reared in samples in which the parasitoid species was also reared. We emphasize that our host assignments must not be taken as definite records (Shaw 1994).

Statistical analyses

A main host plant/insect was defined if 80% of reared individuals originated from this host. Sampling effort for a particular plant species may be assessed as either the number of samples obtained, or the sum of seeds collected, or the total weight of seeds. To examine which plant species were rarely attacked by insects, we considered species with a high number of seeds collected but none attacked (i.e. no insect reared from the seeds), as this variable is more directly relevant to the regeneration of the plant species. We considered the distribution of the number of seeds free of attack for each tree species, ranked in decreasing number. Host species 'rarely attacked' were defined as species belonging to the first quartile of this distribution. It was more challenging to define host species 'heavily attacked' and for this we considered insect load on their hosts both in term of species richness and abundance. With regard to insect species richness, we considered for each host species, the number of insect species reared from a main host, excluding insect singletons. With regard to insect abundance, we considered the number of insects reared per seed (per unit seed), to reduce the effect of sampling effort, and calculated these values for hosts relatively well sampled (for which > 75 seeds were collected). We compared the abundance in the KHC permanent plot of rarely vs. heavily attacked tree species (abundance not defined for liana species) with Mann-Whitney tests for the variables Number of stems (i.e. number of individuals per tree species) and Basal area (i.e. total cross-sectional area of all stems in the plot measured at breast height).

Our analyses about insect inter-annual variation in abundance are limited by only 3 years of data, but motivated by the lack of data for tropical species other than those attacking dipterocarp seeds (i.e. Nakagawa *et al*. 2003). We used the stability index of Wolda (1983) to estimate the magnitude of change in insect abundance between study years (2013-2015). The index is calculated as the natural logarithm of the variance in the natural logarithms of the abundances (+1) of the individuals species. We included insect species reared from the 10 focal families plus the Dipterocarpaceae for these analyses and considered the average number of insects reared per seed among samples obtained each year as a measure of insect abundance. We tested for differences in the average stability index of species (a) of pulp vs. seed eaters, (b) reared from dipterocarps vs. non-dipterocarps, and (c) reared from fleshy vs. dry fruits with Mann-Whitney tests. For (b) and (c) we considered only insects reared from a main host, in order to relate unequivocally insect species to either plant family or seed syndrome. Raw data (abundance per year) for insect species are indicated in Appendix S1.

We evaluated the influence of host plant phylogeny on our results as follows. First, we estimated the phylogenetic relationships between host species present at KHC using the software package Phylomatic (Webb & Donoghue 2005; details in Basset *et al*. 2018). Second, we tested for phylogenetic signal for all tree species attacked, for trees rarely or heavily attacked, and for host trees from which Ichneumonoidea were reared. We calculated the D statistic for phylogenetic signal in a binary trait (Fritz & Purvis 2010). The value of the D statistic is based on the sum of changes between sister clades across the phylogeny. Highly clumped traits tend to have lower D values, closer to 0. We compared the scaled value of the observed D statistic to values generated under a simulated Brownian model of phylogenetic structure and one resulting from no phylogenetic structure (each with 10,000 permutations) using the R package ‘Caper’ (Orme 2013). We used a complementary significance-based approach to provide further support for these results, by testing for phylogenetic signal according to the mean phylogenetic distance (MPD) between tree species. We used standardized effect sizes of MPD generated under null models of tip label randomization (999 runs) as implemented in the R package ‘Picante’ (Kembel *et al*. 2010).

RESULTS

Faunal composition and occurrence of pests and beneficial insects

During the three-year study, we collected 1,970 samples comprising 343.2 kg or 39,252 seeds/fruits from 357 liana and tree species (and a few herbs) representing 66 plant families.

From these samples we reared 17,555 insects (8,851 individuals from the 10 focal plant families). There was a relatively high incidence of Alysiinae (Hymenoptera: Braconidae) and a relatively low incidence of Bruchinae (Coleoptera: Chrysomelidae), Baridinae (Coleoptera: Curculionidae), Cosmopterigidae (Lepidoptera), and Sesiidae (Lepidoptera) in comparison with sites in Panama and Papua New Guinea (Basset *et al.* 2018). Appendix S1 details the 243 species (totaling 8,949 individuals) in the guilds of seed/pulp eaters and parasitoids that we were able to identify or morphotype. About 71% of the morphospecies could be identified to genus and 28% of them to species. This material included mostly beetles, with Curculionidae (53 spp. and 5,644 individuals; including 22 spp. and 4,262 individuals of Scolytinae) and Anthribidae (8 spp. and 396 individuals) predominating. Tephritidae and Stratiomyidae represented 26 and 8 species, and 814 and 464 individuals, respectively. Moths were dominated by Tortricidae (16 spp., 337 indivdiuals), Crambidae (15 spp., 321 individuals) and Pyralidae (14 spp., 390 individuals), while Braconidae were represented by 54 species and 344 individuals (Appendix S1). Most of the insects reared were pulp eaters (127 spp., 73.7% of individuals), followed by seed eaters (55 spp., 22.5%) and parasitoids (62 spp., 4%; Appendix S1). Among pulp eaters, two species of *Coccotrypes* were the most abundant and reared from numerous hosts, whereas the most abundant seed eater was an unidentified species of *Aclees* reared mostly from *Mucuna phaseoleae* (Fabaceae). Note that the scolytines *C. carpophagus*, *C. dactyliperda* and *C. gedeanus* may be considered as seed eaters rather than pulp eaters (Appendix S1). In addition, 796 specimens of Tineidae and Blastobasidae were reared from 56 host species, but the larvae of these families are more likely to be scavengers. We reared at least one species of *Lateantenna* (Blastobasidae, *L. inana* (Butler, 1881)), one of *Opogona* (Tineidae), three of *Phaeoses* (Tineidae), and one of *Tineovertex* (Tineidae).

Of the 69 taxa identified to species-level, 30 (43%) may be considered pests (Appendix S1). This includes two ambrosia beetles that usually do not breed in seeds. The insect taxa in which the proportions of reported pest species to species identified were highest included: Nanophyidae (100%), Crambidae (67%), Tortricidae (55%), Scolytinae

(36%), and Tephritidae (26%). The origin of these pest species is summarized in Fig. 1. Most pests were seed eaters, and were reared mostly from Dipterocarpaceae and from hosts with seed syndromes C1 (dry winged seed) and A1.2 (fleshy drupe with thin mesocarp). Most pest species and individuals were reared from dry fruits as opposed to fleshy fruits (Fig. 1). Only one pest of stored products, *Pyralis pictalis*, was reared from the seeds and fruits collected in the Khao Chong forest.

We obtained 57 samples from seven of 13 dipterocarp species growing at KHC, totaling 1,240 seeds (10.3 kg; 3.1% of total seeds reared), which yielded 425 insects (14 samples lacked insects). Out of these, we obtained 236 weevils and moths whose individual larvae likely feed on and kill a single seed (Hosaka *et al*. 2009). This suggests that about 19% of dipterocarp seeds were lost to weevils and moths. Insects reared from dipterocarp seeds included at least 26 species of seed and pulp eaters (Appendix S2), mostly belonging to the Curculionidae, Nanophyidae and Tortricidae. The most abundant species were an unidentified species of *Alcidode*s (Curculionidae) reared from *Parashorea* *stellata*, and *Andrioplecta shoreae* reared from four dipterocarp hosts. In comparison Nakagawa *et al*. (2003) reared 1,419 insects representing 51 species from 20,215 seeds of 24 dipterocarp species in Sarawak. Only four species were in common between their study and ours (Appendix S2). In Pasoh, Malaysia, Hosaka *et al*. (2009) recorded at least 32 insect species from two consecutive mast-fruiting events of 15 species of dipterocarps (3,779 insects reared from 27,483 seeds). Senthilkumar *et al*. (2009) studied seed predation in *Dipterocarpus retusa* in Assam, India, and recorded nine species of seed predators. In Thailand, at least 12 species of seed predators have been recorded from dipterocarps (Hutacharern & Tubtim 1995; DNP 2018). Because of incomplete identifications, different taxonomists studying the insect material and inconsistent use of DNA barcoding, it is difficult to compare the lists of taxa provided by these dipterocarp studies. Nonetheless, they suggest a relatively low overlap with the fauna feeding on dipterocarp seeds at KHC. The densities of reared insect individuals per dipterocarp seed appears to be higher at Khao Chong during the study period (0.34 insect per seed) compared with Lambir Hills (0.07

insect per seed; Nakagawa *et al*., 2003) or Pasoh (0.14 insect per seed; Hosaka *et al*. 2009), during periods of mast fruiting. One species of Blastobasidae and two species of Tineidae were reared from Dipterocarpaceae at KHC.

Of 27 parasitoid species for which we could identify the main insect hosts and verify whether the host was considered a pest of fruits or seeds, 5 species (18.5%) could be considered beneficial (Appendix S1). All these species were Opiinae attacking *Bactrocera* pests (Tephritidae) breeding in the fruits of many host plant species. In addition, the larvae of *Hermetia illucens* recycle manure, so this species can be also considered beneficial (Appendix S1).

Levels of parasitism of insects attacking seeds and fruits

Our data allowed us to present only crude estimates of the level of parasitism due to Ichneumonoidea (mostly Braconidae, Appendix S1 and Table 1). Overall, about 8.2% and 2.9% of insect species and individuals were parasitized, respectively. The level of parasitism was not notably different between pulp and seed eaters (Fisher exact test, p = 0.483). Tephritidae was the most commonly attacked family by Braconidae, followed by Curculionidae (not including Scolytinae). *Bactrocera irvingiae* and *Andrioplecta shoreae,* reared from several host plant species, appeared to be the species most commonly parasitized by braconids. Insect taxa that appeared to be infrequently parasitized (Table 1: Stratiomyidae, Pyralidae, Crambidae, Scolytinae) may be under attack by parasitoids other than braconids. For example, *Coccotrypes* spp. (Scolytinae) are known to be attacked by the braconid genera *Spathius*, *Bracon* and *Diospilus* (Quicke, 2015). These genera were infrequently reared at Khao Chong and obtained from other putative hosts. We also note that there was no obvious correlation between the number of species of parasitoids and prey reared from particular plant families (only main hosts considered: Spearman rank correlation, $r_s = 0.112$, $p > 0.25$, $n = 31$ plant families). Finally, most species of parasitoids were reared from main host plant species with syndrome A1.2 (40.9% of species), B1 (25.0%) and A2.2 (18.2%).

Rates of seed attack

Of 357 plant species surveyed, seeds/fruits of 101 were free of attack (28.3%). The first quartile of the distribution of these species represented 71% of the total number of seeds not attacked. *Antidesma neurocarpum* (Phyllanthaceae) was the most avoided plant species, with 344 seeds not attacked (Fig. 2). Other tree species rarely attacked (first quartile of the distribution in Fig. 2) included 11 Rubiaceae, 9 Annonaceae, 9 Arecaceae, 7 Meliaceae, and 6 Euphorbiaceae, Fabaceae and Phyllanthaceae each. Plant families with a high proportion of seeds not attacked (> 15%) included Apocynaceae, Clusiaceae, Meliaceae, Anacardiaceae, Rubiaceae, Celastraceae, Phyllanthaceae, Sapotaceae (Fig. 2). Of those, Phyllanthaceae, Rubiaceae and Meliaceae were species-rich and collected with a high sampling effort, and hence, may be considered as families relatively infrequently attacked by insects. Seed syndrome B2 (non-fleshy) also had a relatively high proportion of seeds free of attack (Fig. 2).

The main hosts of insects at KHC (as defined in the methods) belonged to 40 species and 16 plant families. Only *Parashorea stellata* (Dipterocarpaceae) and *Lepisanthes rubinigosa* (Sapindaceae) supported more than two insect species. Dipterocarpaceae, Annonaceae and Fabaceae had a relatively high load of insect species, as well as seed syndromes B1, A1.2 and C1, a mixture of dry and fleshy fruits (Fig. 3a). The 25 most heavily attacked host species (in terms of insect abundance) often belonged to Annonaceae, Fabaceae, Sapindaceae and Myristicaceae (Fig. 3b). The highest numbers of insect reared were obtained from *Mezzettia parviflora* (Annonaceae). Overall densities of insects were also relatively high on Meliaceae and Anacardiaceae (Fig. 3c). On average the highest densities of insect reared per seed and plant species were obtained from hosts with Syndrome C2 (multiple dry seeds). There was no significant difference between the number of stems in the plot of tree species rarely and heavily attacked (Mann-Whitney $U = 192.5$, $p = 0.808$). However heavily attacked tree species had significantly larger basal areas in the plot than rarely attacked tree species ($U= 309.0$, $p < 0.001$; mean ± s.e. = 6.08

m^{-2} ± 1.145 and 1.28 m^{-2} ± 0.439, respectively).

Insect fluctuation during study years

Overall the highest densities per unit seed over the three-year study were attained by several species of Scolytinae (Appendix S1). There was no significant difference between the average stability index of pulp-eating species and that of seed-eating species (Mann-Whitney test, U = 1481.5, p = 0.927). However, the average stability index of species reared from dipterocarp hosts was significantly smaller (more stable) than that of species reared from non-dipterocarp hosts (U= 710.0, p = 0.027; Fig. 4a). Further, the average stability index of species reared from fleshy fruits was significantly smaller (more stable) than that of species reared from dry fruits (U=313.0, p=0.010; Fig. 4b).

Host plant phylogenetic signals

Fig. 5 provides a visual interpretation of how all/rarely/heavily attacked plant species, and from which Ichneumonoidea were reared, clustered across the whole plant phylogeny at KHC. The three first categories showed a limited phylogenetic signal with the D statistic relatively high (all plant species attacked: D=0.862, p(D>0)=0.0001, p(D<1)=0.0001; species rarely attacked: D=0.781, p(D>0)=0.005, p(D<1)=0.0023; species heavily attacked: D=0.855, p(D>0)=0.025, p(D<1)=0.0001). For plant species hosting Ichneumonoidea, there was clearly no phylogenetic signal (D= 0.994, p(D>0)=0.418, p(D<1)=0.0001). Significance tests of phylogenetic signal according to MPD indicated that all categories were not clumped across plant phylogeny (all species: MPD observed = 358.9, MPD random mean = 342.5, p = 0.92; species rarely attacked: MPD observed = 305.3, MPD random mean = 328.1, p = 0.23; species heavily attacked: MPD observed = 364.8, MPD random mean = 329.6, p = 0.88; species hosting Icheumonoidea: MPD observed = 355.9, MPD random mean = 330.3, p = 0.78).

DISCUSSION

Insect assemblages feeding on seeds and fruits in tropical rainforests are challenging to study, primarily because of low rates of attack, high plant diversity, and the high sampling effort required to rear sufficient numbers of insect specimens to provide meaningful statistics (Ctvrtecka *et al*. 2014). Further, the taxonomic knowledge of insects reared from native seeds and fruits of tropical countries is often limited (Nakagawa *et al*. 2003; Miller *et al*. 2014). Regarding the questions asked in this study, we observed that (1) about 43% of species identified could be considered pests. Most were seed eaters, particularly on dry fruits (but only a single pest of stored products was recorded), belonging to Nanophyidae, Tortricidae, Crambidae, Scolytinae and Tephritidae. (2) About 19% of parasitoid species for which we could assess whether the main insect host is a pest could be considered beneficial. All these species were Opiinae with *Bactrocera* pests breeding in fruits as main hosts. (3) Overall about 8% of insect species reared from seeds/fruits were parasitized by Ichneumonoidea, with Tephritidae being the family most commonly attacked. (4) The seeds/fruits of about 28% of plant species in the KHC forest were free of attack. The seeds/fruits of Phyllanthaceae, Rubiaceae and Meliaceae were attacked relatively infrequently by insects. In contrast, fruits and seeds of species of Annonaceae, Fabaceae, Sapindaceae and Myristicaceae were more likely to be heavily attacked, with multiple dry seeds (Syndrome C2) often well attacked. There was no apparent effect of plant phylogeny on rates of attack but heavily attacked tree species had larger basal area in the KHC plot than rarely attacked tree species. (5) The highest densities per unit seed over the three study years were attained by several species of Scolytinae, as these beetles may produce large brood inside fruits. Insects reared from fleshy fruits were more likely to exhibit relatively stable populations compared to insects reared from dry fruits, except for insects reared from dipterocarps, which appeared to have relatively stable populations during the study years at KHC.

The proportion of pest species recorded in our study is probably inflated because in the tropics insect pests are far better known than native forest insects, especially those reared from native seeds and fruits (Miller *et al.* 2014). We encountered two general categories of pests: (1) various beetles species breeding in the dry seeds of dipterocarps that appear to be rather specific (Nakagawa *et al*. 2003) and (2) polyphagous species of Tephritidae breeding in fleshy fruits. The former species could be of concern because modest dipterocarp plantations have been established in Thailand since the 1980s (Weinland 1998). However, densities of the most common pest feeding on dipterocarps, *Alcidodes* sp. 15, were rather low, reaching 0.16 insect per seed on average during the three-year study. *Bactrocera irvingiae* was the most commonly reared tephritid from fleshy fruits, but this species is not considered a pest. *Dacus longicornis*, a pest of Cucurbitaceae, reached densities of 0.44 flies per fruit on our focal hosts, but was not very abundant when all plant species surveyed were considered. We conclude that during our study years the KHC forest did not support insect pests in densities that may cause concern to timber species (dipterocarps) or fruit crops. Less than 20% of parasitoid species appeared to have insect pests as hosts. Since we have little evidence that the KHC forest acts as a reservoir of insect seed/fruit pests, it is difficult to argue that the same forest acts as a reservoir of beneficial insect species. A better test of this issue would be to compare parasitoid and seed insect assemblages in commercial crops contiguous with natural forests, such as in Mexico (Aluja *et al.* 2014). However, in Thailand such situations are rare, with habitats contiguous to natural forests represented primarily by buffalo fields, maize plantations, or holiday resorts (DJ Quicke, pers. obs.).

A more interesting question related to parasitoids is whether some seed insects may be relatively free of ichneumonoid parasitoids. In Costa Rica, Janzen (1980) observed that Bruchinae seed predators are rarely attacked by parasitoids. At KHC Bruchinae are replaced by Anthribidae and Curculionidae (Basset *et al*. 2018), whose species frequently were attacked (except for Scolytinae, Table 1). Further, many of the Tephritidae species were attacked by braconids. We reared about 50% fewer individuals of Stratiomyidae (Appendix S1) but did not record any braconid attacks on these flies. There are very few Ichneumonoidea parasitoids of Stratiomyidae (Quicke 2015), which are attacked only as eggs by various Chalcididae and Trichogrammatidae (Robertson 1987). We also note that there was no obvious correlation (negative or positive) between the number of prey and parasitoids reared from particular plant families, and that there was no phylogenetic signal relating host plant species from which Ichneumonoidea were reared. Although these represent weak tests of the nasty host hypothesis (Gauld *et al*. 1992), these observations do not appear to support it (and see Quicke 2012 for other considerations). Our rearing scheme, albeit imperfect to obtain reliable data about the identity of parasitoid hosts and level of parasitism, nevertheless suggests that the action of parasitoids at KHC may be too infrequent to induce strong differences in seed/fruit crops, with possible consequences on local tree abundance.

There are certainly different reasons for seeds of particular plant species to be attacked less frequently by insects. First, plant chemistry may be an important determinant; because seeds represent the most valuable part of the plant, they are usually well protected (Janzen 1969; Ramírez & Traveset 2010). At present we lack data for most KHC plant species to provide a context for discussing plant chemistry (see Gripenberg *et al*. 2018 for such a discussion). Our phylogenetic tests indicated only limited phylogenetic signal for the categories of plant species attacked by seed and pulp eaters, as well as for plant species rarely of heavily attacked. This suggests that insects overall may not be very selective regarding attacking or avoiding particular clades of plant species, even if they may be reasonably host specific. Second, sample size is certainly important (Ctvrtecka *et al*. 2014), but among our focal plant families, we could nevertheless crudely assign species to the categories rarely and heavily attacked. The next important variable is probably local host abundance. We found that host species heavily attacked have on average a higher basal area (but not number of stems) in the KHC plot than rarely attacked host species. This suggests that seed and pulp eaters are influenced primarily by seed/fruit production, which is probably more dependent on basal area than on number of stems. It seems less likely that seed and pulp eaters are directly limiting the local abundance of heavily attacked tree species.

The observations that dipterocarp mast fruiting does not occur at Khao Chong

(Kurten *et al*. 2017), and insect densities in dipterocarp seeds during the study years were higher than in Malaysian dipterocarp forests experiencing mast fruiting (Nakagawa *et al*. 2003; Hosaka *et al*. 2009), support the hypothesis of satiation of seed predators by mast fruiting (Curran & Webb 2000). However, it is not clear why insects reared from dipterocarp seeds at KHC should have more stable populations than insects reared from non-dipterocarp hosts. This may be related to easy host-switching and alternative hosts for insects feeding on dipterocarp seeds (Nakagawa *et al*. 2003). The low faunal turnover between dipterocarp insects at Khao Chong and in Malaysia is also of interest, suggesting that different insect assemblages may be well adapted to either mast-fruiting events or the lack of these events. We also strongly suspect that low host specificity in insects breeding in fleshy fruits may explain the more stable populations of these species as opposed to those breeding in dry fruits. This issue will be explored elsewhere with more adequate data.

In conclusion, most of the evidence (often indirect) suggests that insects feeding on seeds and fruits at Khao Chong have a limited impact on host abundance in this forest.

Insect densities were low, as was the number of confirmed insect pests, and heavily attacked tree species were not notably less abundant than other species. This situation appears similar to that described for a lowland rainforest in Papua New Guinea (Ctvrtecka *et al*. 2014; Sam *et al*. 2017). This could be a consequence of the high plant diversity at these two locations, but it also may be related to the relative occurrence of fleshy vs. dry fruits (Basset *et al.* 2018). It is obvious that more surveys of insects feeding on seeds and fruits are required at different rainforest locations to discuss adequately this issue.

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REFERENCES

Anderson-Teixeira KJ, Davies SJ, Bennett AC, Gonzalez-Akre EB, Muller-Landau HC, Wright SJ,.. Zimmerman J (2014) CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology* **21,** 528-–549.

Allwood AJ, Chinajariyawong A, Kritsaneepaiboon S, Drew RAI, Hamacek EL, Hancock DL, Hengsawad C, Jipanin JC, Jirasurat M, Kong Krong C, Leong CTS, Vijaysegaran S (1999) Host plant records for fruit flies (Diptera: Tephritidae) in southeast Asia. *The Raffles Bulletin of Zoology* Supplement no. **7,** 1–92.

Aluja M, Sivinski J, Van Driesche R, Anzures-Dadda A, Guillén L (2014) Pest management through tropical tree conservation. *Biodiversity and Conservation* **23,** 831–853.

Baltzer JL, Davies SJ (2012) Rainfall seasonality and pest pressure as determinants of tropical tree species' distributions. *Ecology and Evolution* **2,** 2682–2694.

Basset Y, Dahl C, Ctvrtecka R et al. (2018) A cross-continental comparison of assemblages of seed- and fruit-feeding insects in tropical rainforests: faunal composition and rates of attack. *Journal of Biogeography* **45,** 1395–1407.

Browne FG (1961) The biology of Malayan Scolytidae and Platypodidae. *Malayan*

Forest Records **22,** 1–255.

Bunyavejchewin S, Baker PJ, Davies SJ (2011) Seasonally dry tropical forests in continental Southeast Asia: Structure, composition, and dynamics. In: McShea WJ, Davies SJ, Bhumpakphan N (eds) The ecology and conservation of seasonally dry forests in Asia, pp 9–35. Smithsonian Institution Scholarly Press, Washington, D.C.

Copeland RS, Luke Q, Wharton RA (2009) Insects reared from the wild fruits of Kenya. *Journal of East African Natural History* **98,** 11–66.

Ctvrtecka R, Sam K, Brus E, Weiblen GD, Novotny V (2014) Frugivorous weevils are too rare to cause Janzen– Connell effects in New Guinea lowland rainforest. *Journal of Tropical Ecology* **30,** 521–35.

Ctvrtecka R, Sam K, Miller SE, Weiblen GD, Novotny V (2016) Fruit sizes and the structure of frugivorous communities in a New Guinea lowland rainforest. *Austral*

Ecology **41,** 228–237.

Curran LM, Webb CO (2000) Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs* **70**, 129–148.

DNP (2018) Dipterocarps and their insect seed predators. National Parks, Wildlife and Plant Conservation Department. Available from URL: www.dnp.go.thdipinsDipterocarpsAndTheirInsectSeedPredators.htm

Doorenweerd C, Leblanc L, Norrbom AL, San Jose M, Rubinoff D (2018) A global checklist of the 932 fruit fly species in the tribe Dacini (Diptera, Tephritidae). *ZooKeys* **730,** 17–54.

Fritz SA, Purvis A (2010) Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proceedings of the Royal Society, Series B, Biological Sciences* rspb20100030.

Gauld ID, Gaston KJ, Janzen DH (1992) Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos* **65,** 353–357.

Gripenberg S, Rota J, Kim J, Wright SJ, Garwood NC, Fricke EC, ... Salminen JP (2018) Seed polyphenols in a diverse tropical plant community. *Journal of Ecology* **106,** 87–100.

Holloway JD (2011) The Moths of Borneo: Families Phaudidae, Himantopteridae and Zygaenidae; revised and annotated checklist. *Malayan Nature Journal* **63,** 1–548.

Holloway JD, Kibby G, Peggie D, Carter DJ, Miller SE (2001) *Families of Malesian moths and butterflies*. Brill, Leiden. xii + 456 pp.

Hosaka T, Yumoto T, Kojima H, Komai F, Noor NSM (2009) Community structure of pre-dispersal seed predatory insects on eleven *Shorea* (Dipterocarpaceae) species. *Journal of Tropical Ecology* **25,** 625–36.

Hosaka T, Yumoto T, Chen YY, Sun IF, Wright SJ, Noor NSM (2011) Abundance of insect seed predators and intensity of seed predation on *Shorea* (Dipterocarpaceae) in two consecutive masting events in Peninsular Malaysia. *Journal of Tropical Ecology* **27,** 651–655.

Hutacharern C, Tubtim N (1995) *Checklist of Forest Insects in Thailand*. Office of Environmental Policy and Planning, Bangkok, Thailand.

Iku A, Itioka T, Kishimoto-Yamada K, Shimizu-kaya U, Mohammad FB, Hossman MY et al. (2017) Increased seed predation in the second fruiting event during an exceptionally long period of community-level masting in Borneo. *Ecological Research* **32**, 537–545.

Janzen DH (1969) Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* **23,** 1–27.

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *The*

American Naturalist **104,** 501–528.

Janzen DH (1971) Seed predation by animals. *Annual Review of Ecology and Systematics* **2,** 465–492.

Janzen DH (1980) Specificity of seed-attacking beetles in a Costa Rican deciduous forest. *The Journal of Ecology* **68,** 929–952.

Janzen DH (1985) A host plant is more than its chemistry. *Illinois Natural History Survey Bulletin* **33,** 141–174.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD *et al.* (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26,** 1463–1464.

Kuroko H, Lewvanich A (1993) *Lepidopterous pests of tropical fruit trees in Thailand* (with Thai text). Japan International Cooperation Agency, Tokyo.

Kurten EL, Bunyavejchewin S, Davies SJ (2017) Phenology of a dipterocarp forest with seasonal drought: Insights into the origin of general flowering. *Journal of Ecology* **106,** 126–136.

Lewis OT, Gripenberg S (2008) Insect seed predators and environmental change. *Journal of Applied Ecology* **45,** 1593–1599.

Lyal CHC, Curran LM (2000) Seed-feeding beetles of the weevil tribe Mecysolobini (Insecta: Coleoptera: Curculionidae) developing in seeds of trees in the Dipterocarpaceae. *Journal of Natural History* **34,** 1743–1847.

Miller SE, Copeland RS, Rosati ME, Hebert PD (2014) DNA barcodes of microlepidoptera reared from native fruit in Kenya. *Proceedings of the Entomological Society of Washington* **116,** 137–142.

Nakagawa M, Itioka T, Momose K, Yumoto T, Komai F, Morimoto K, ... Inoue T (2003) Resource use of insect seed predators during general flowering and seeding events in a Bornean dipterocarp rain forest. *Bulletin of Entomological*

Research **93,** 455–466.

Nakagawa M, Takeuchi Y, Kenta T, Nakashizuka T (2005) Predispersal seed predation by insects vs. vertebrates in six dipterocarp species in Sarawak, Malaysia. *Biotropica* **37,** 389–396.

Novotny V, Basset Y, Miller SE, Weiblen GD, Bremer B, Cizek L, Drozd P (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature* **416,** 841–844.

Orme D (2013) The caper package: comparative analysis of phylogenetics and evolution in R. R package version 5,1–36.

Quicke DLJ (2012) We know too little about parasitoid wasp distributions to draw any conclusions about latitudinal trends in species richness, body size and biology. *PLoS One* **7,** e32101.

Quicke DLJ (2015) *The Braconid and Ichneumonid Parasitoid Wasps: Biology,* *Systematics, Evolution and Ecology*. John Wiley, Chichester, U.K.

Ramírez N, Traveset A (2010) Predispersal seed predation by insects in the Venezuelan central plain: overall patterns and traits that influence its biology and taxonomic groups. *Perspectives in Plant Ecology, Evolution and Systematics* **12,** 193–209.

Ratnasingham S, Hebert PDN (2013) A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. *PloS One* **8,** e66213.

Robertson LN (1987) The effects of natural enemies on the population dynamics of sugarcane soldier fly, Inopus rubriceps (Dip.: Stratiomyidae). *Agriculture, Ecosystems & Environment* **19,** 343–363.

Russell EP (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environmental Entomology* **18,** 590–599.

Sam K, Ctvrtecka R, Miller SE, Rosati ME, Molem K, Damas K, ... Novotny V (2017)

Low host specificity and abundance of frugivorous Lepidoptera in the lowland rain forests of Papua New Guinea. *PloS One* **12,** e0171843.

Senthilkumar N, Barthakur ND, Singh AN (2009) Record of seed insect pests of *Dipterocarpus retusus* in Hollongapar reserve forests, Assam. *Journal of Tropical Forest Science* **21,** 8–12.

Shaw MR (1994) Parasitoid host ranges In: Hawkins BA, Sheehan W (eds) *Parasitoid Community Ecology*, pp 111–144. Oxford University Press, Oxford.

Stephenson AG (1981) Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* **12,** 253–279.

Subramanyam B (ed) (1995) *Integrated Management of Insects in Stored Products*. CRC Press, Boca Raton.

Turgeon JJ, Roques A, Groot PD (1994) Insect fauna of coniferous seed cones: diversity, host plant interactions, and management. *Annual Review of Entomology*

39, 179–212.

Webb CO, Donoghue MJ (2005) Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes* **5,** 181–183.

Weinland G (1998) Plantations In: Appanah S, Turnbull JM (eds*) A Review of Dipterocarps: Taxonomy, Ecology and Silviculture*, pp 151–186. CIFOR, Bogor.

Wolda H (1983) “Long-term” stability of tropical insect populations. *Researches on Population Ecology* **25,** 112–126.

Zehnder G, Gurr GM, Kühne S, Wade MR, Wratten SD, Wyss E (2007) Arthropod pest management in organic crops. *Annual Review of Entomology* **52,** 57–80.

Zhang BC (1994) *Index of Economically Important Lepidoptera*. CAB International, Wallingford.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details of insects reared from seeds and fruits and Khao Chong.

Appendix S2. Seed and pulp eaters reared from Dipterocarpaceae at Khao Chong.

Figure legends

Figure 1 Source of pest species recorded at Khao Chong, detailed for species and individuals and by (a) insect families, (b) insect guilds, (c) main host family and (d) main host seed syndromes. Curculionoidea do not include Scolytinae, which are indicated separately.

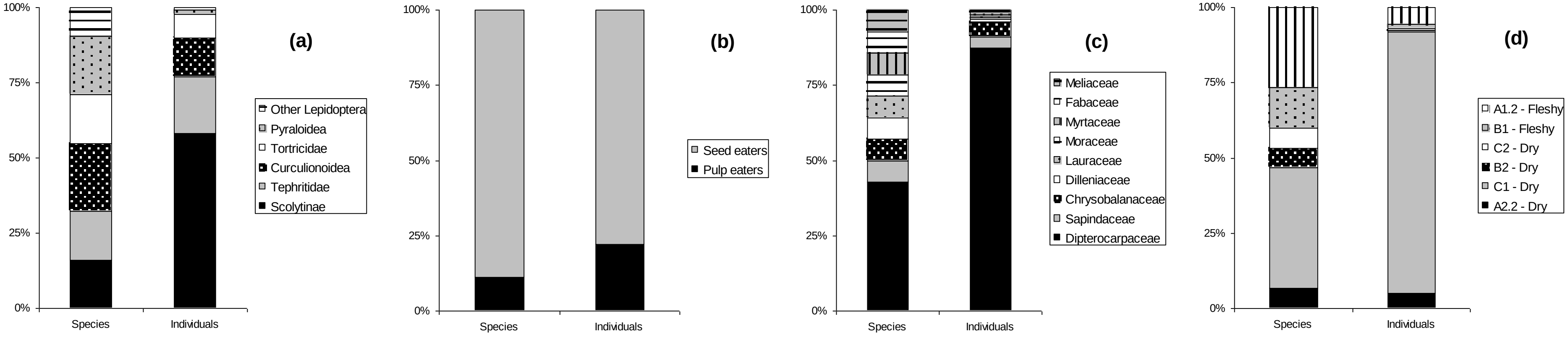
Figure 2 Plant species free of seed attack. (a) Inset: full distribution of the number of seeds free of attack for each species not attacked; main figure: first quartile of the distribution with name of species detailed and plant families abbreviated and colored similarly. (b) Proportion of seeds free of attack (black) detailed by plant family (when no. of plant species surveyed ≥ 3). (c) Same, detailed by seed syndrome. Abbreviations of plant families: An=Anacardiaceae; Ao=Annonaceae; Ap=Apocynaceae; Ar=Arecaceae; Cl=Clusiaceae; Er=Erythroxylaceae; Eu=Euphorbiaceae; Ge=Gentianaceae;

La=Lauraceae; Lo=Loganiaceae; Ly=Lythraceae; Me=Meliaceae; Mo=Moraceae; Ph=Phyllanthaceae; Po=Poaceae; Ru=Rubiaceae; Un=Unknown.

Figure 3 Heavily attacked plant species. (a) Number of insect species (white = pulp eaters, black = seed eaters) reared from main hosts (as defined in methods), detailed by plant families. Inset: same presentation, detailed by seed syndrome. (b) Number of insects reared per seed for the 25 most attacked plant species. Black = seed eaters, white or different colour = pulp eaters (same colour denotes same plant family). (c) Average number of insects reared per seed and plant species, detailed by plant family (white = pulp eaters, black = seed eaters). (d) Same presentation, detailed by seed syndrome. Abbreviations of families for (b): An=Anacardiaceae; Ao=Annonaceae; Ar=Arecaceae; Ch=Chrysobalanaceae; Di=Dilleniaceae; Di=Dipterocarpaceae; Eb=Ebenaceae; Eu=Euphorbiaceae; Fa=Fabaceae; La=Lauraceae; Me=Meliaceae; Mo=Moraceae; My=Myristicaceae; Ru=Rubiaceae; Sa=Sapindaceae.

Figure 4 Insect species ranked by their stability index. (a) Species reared from non-dipterocarp hosts (grey bars) vs. species reared from dipterocarp hosts (black bars). (b) Species reared from fleshy fruits (grey bars) vs. dry fruits (black bars).

Figure 5 Maximum clade credibility consensus trees depicting the phylogenetic relationships between 622 host plant species, with for each consensus tree, taxa marked in red indicate (a) all species attacked, (b) species rarely attacked, (c) species heavily attacked and (d) species from which Ichneumonoidea were reared.



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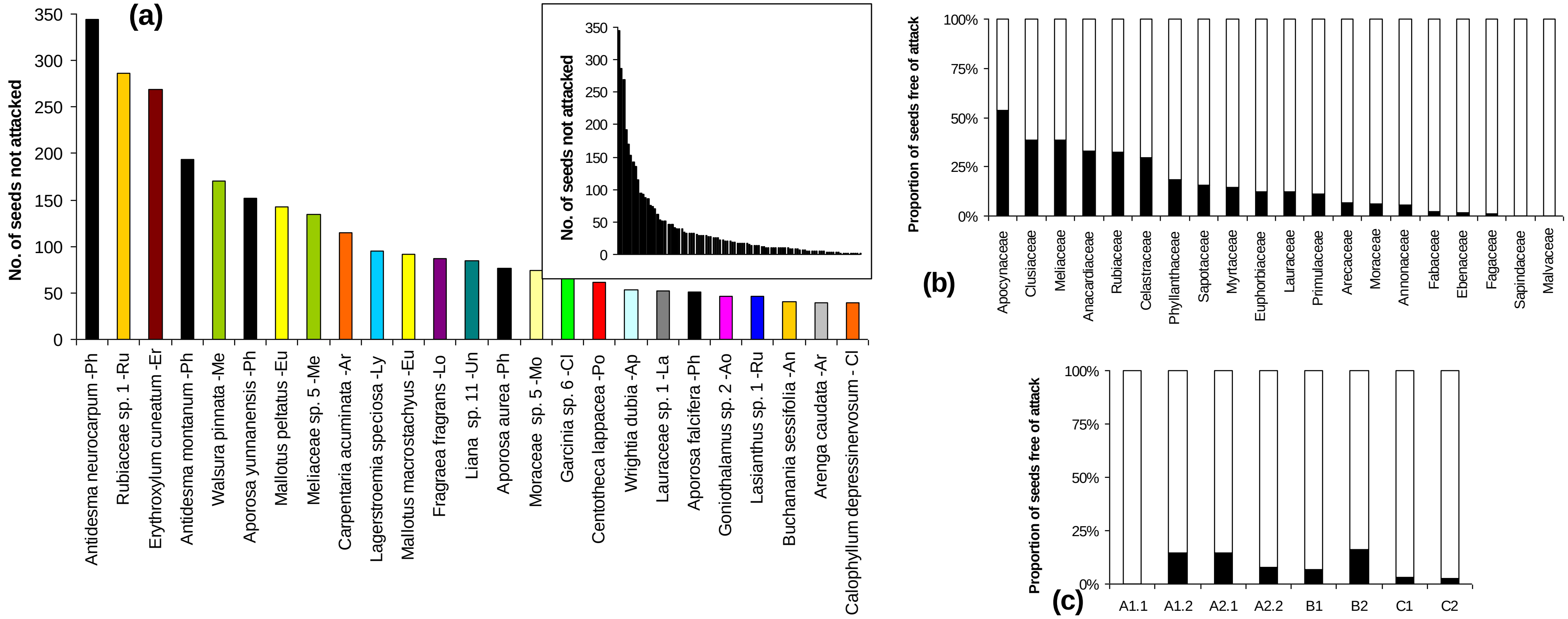

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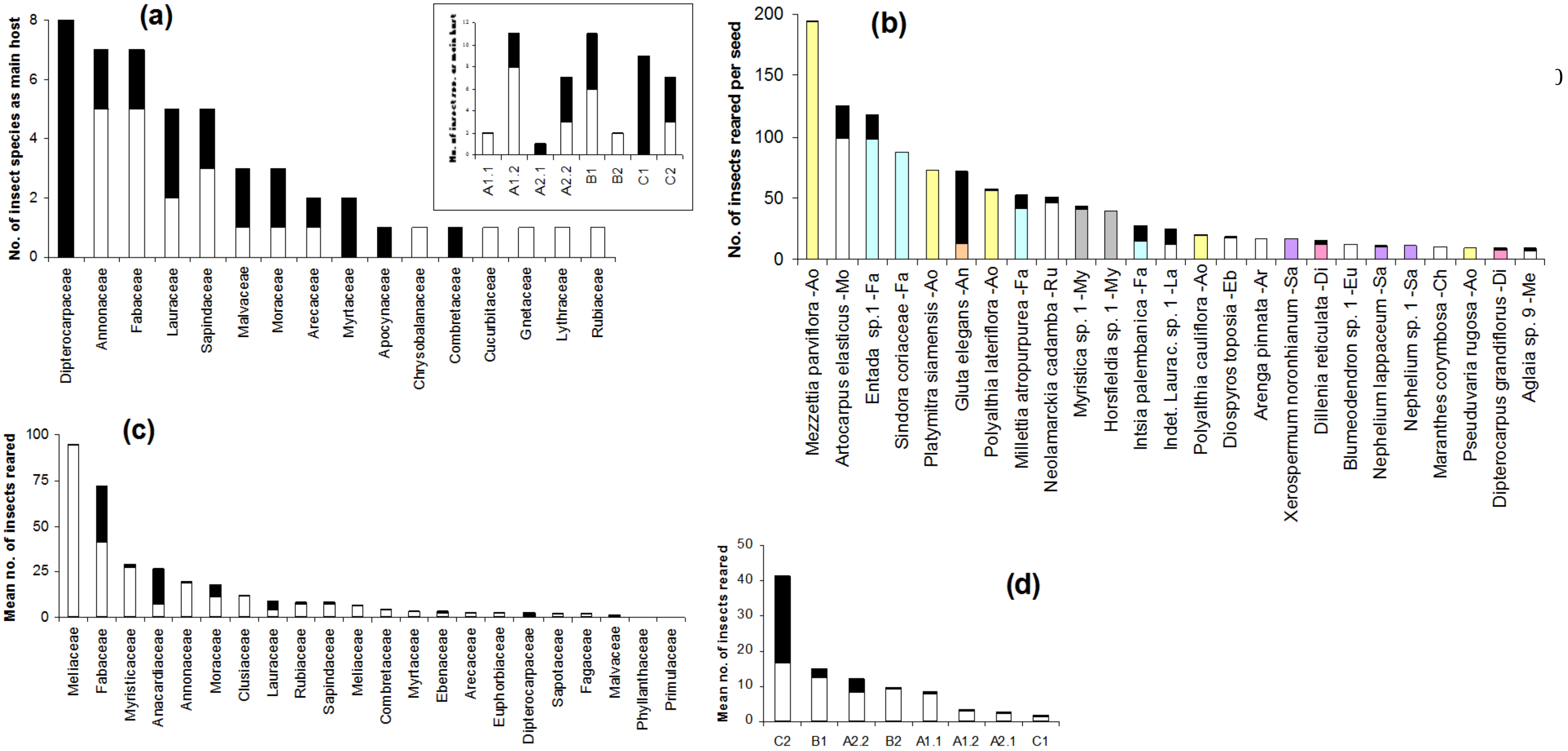

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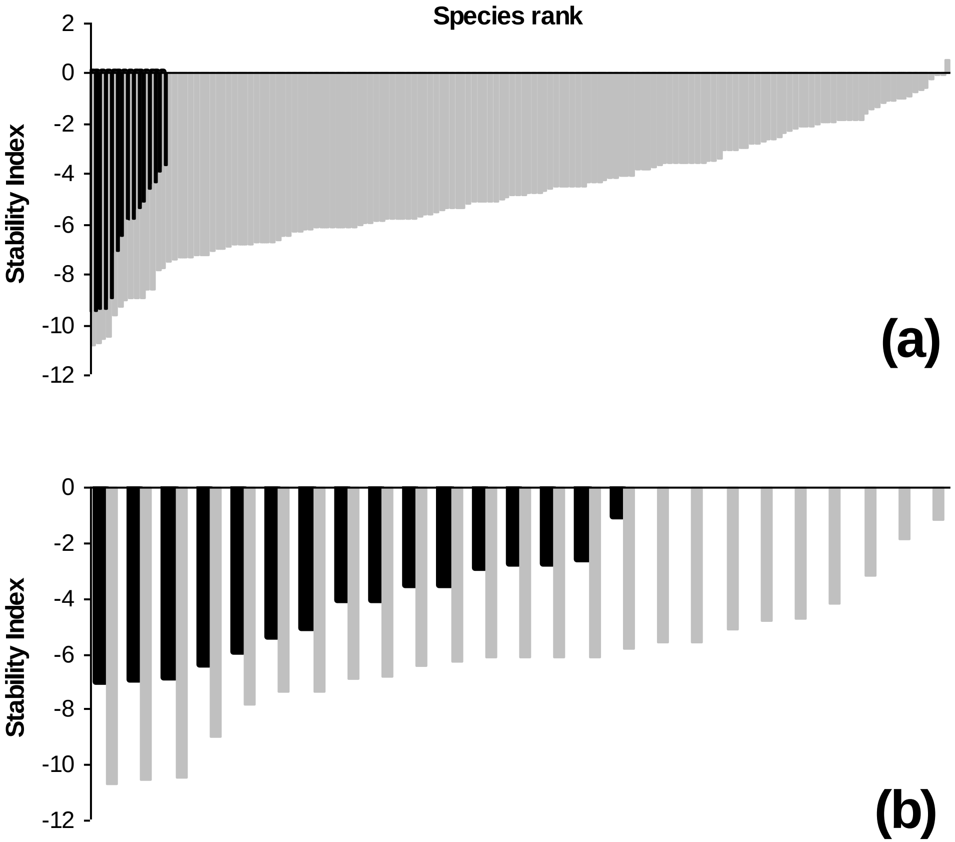

Figure 4 Insect species ranked by their stability index. (a) Species reared from non-dipterocarp hosts (grey bars) vs. species reared from dipterocarp hosts (black bars). (b) Species reared from fleshy fruits (grey bars) vs. dry fruits (black bars).

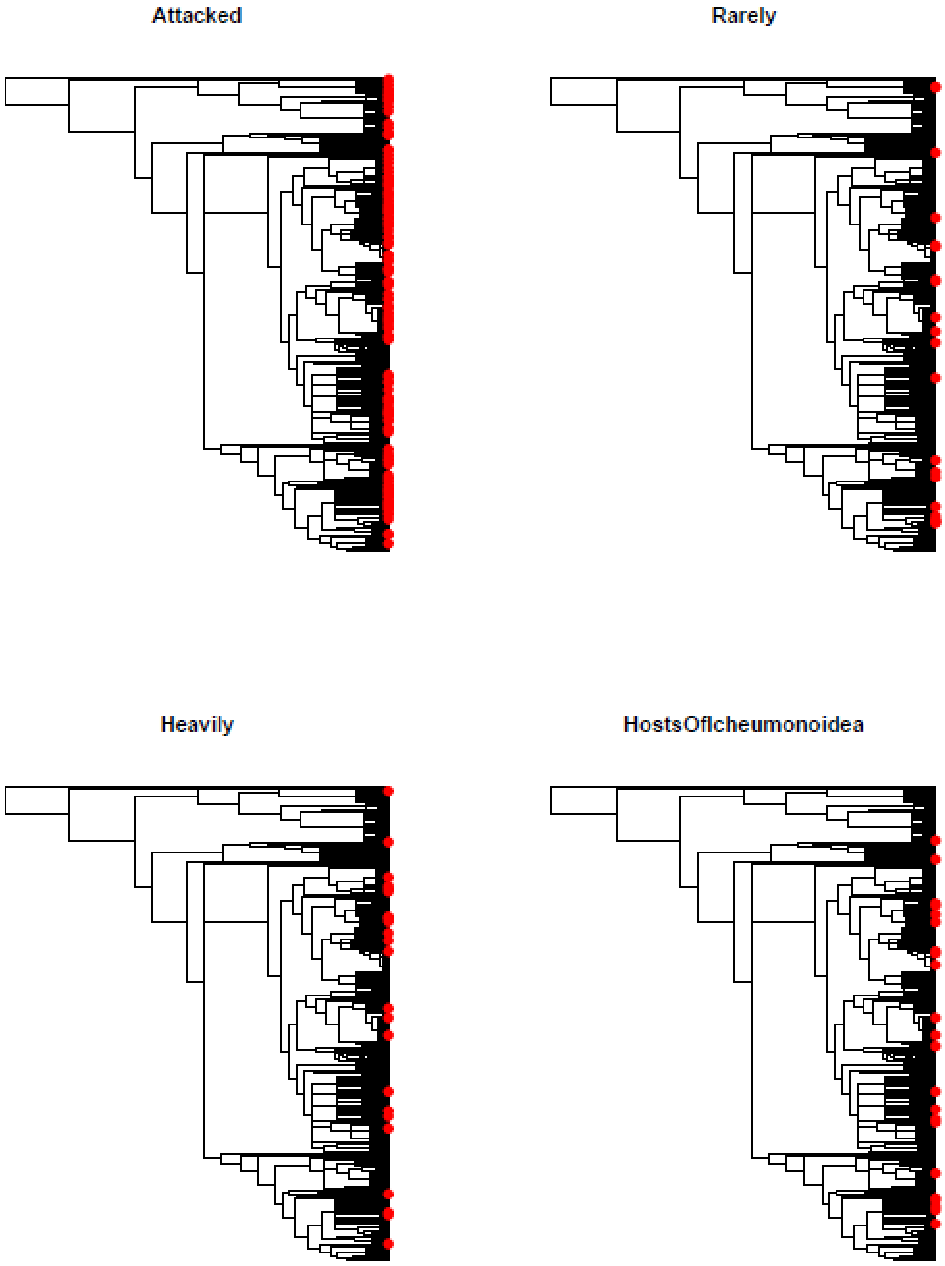

Figure 5 Maximum clade credibility consensus trees depicting the phylogenetic relationships between 622 host plant species, with for each consensus tree, taxa marked in red indicate (a) all species attacked, (b) species rarely attacked, (c) species heavily attacked and (d) species from which Ichneumonoidea were reared.

Table 1 Levels of parasitism due to Ichneumonoidea for the main higher insect taxa reared from seeds and fruits at Khao Chong, presented in decreasing % of species parasited.

Taxa	**No. spp. reared**	**No. spp. parasitized**	**% species parasitized**	**% individuals parasitized**
Tephritidae	26	7	26.9	7.0
Anthribidae	8	1	12.5	0.3
Curculionidae *	26	3	11.5	0.8
Tortricidae	13	1	7.7	4.6
Stratiomyidae	8	0	0	0
Pyralidae	8	0	0	0
Crambidae	15	0	0	0
Scolytinae	22	0	0	0
All pulp eaters	113	8	7.1	6.3
All seed eaters	34	4	11.8	0.7
All	147	12	8.2	2.9

* Without Scolytinae