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The population dynamics and biodiversity of insect seed predators in tropical rainforests of Sarawak

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Abstract Insect seed predators play important roles in the dynamics of forest ecosystems. Here, we briefly review the recent progress of research in ecology and evolutionary biology of insect seed predators in Southeast Asian tropical rainforests, where community-wide supra-annual masting (called "general reproduction (GR)" here) occurs, with the introduction of the predator satiation hypothesis, which is one of the leading hypotheses to explain the ecological mechanisms promoting the evolution of GR. We also introduce our own current studies on insect seed predators in the lowland tropical rainforest at Lambir Hills National Park, Sarawak. In addition, we present our future plans for research on the natural history and evolutionary ecology of interactions between seed-feeding insects and plant species in Sarawakian tropical rainforests, with emphasis on the necessity for the long-term census on the community-level seed predation.

Keywords General flowering, General reproduction, Insect-plant interactions, masting, Plant reproductive phenology, Predator saturation hypothesis

Introduction

Seed predation by insects often affects plant reproduction, with resultant heavy mortality of the seed predator. Therefore, to achieve better understanding of the population dynamics of plants and of the resultant properties of plant assemblages, it is necessary to elucidate the population and community ecology of the insect seed predators, especially the dynamics of interactions between the insect seed predators and their host plants. In addition, the interactions between them are of great interest to evolutionary ecology because the interactions are likely to function as one of the

systems that increases biodiversity. However, there have been few studies on the ecology of insect seed predators in the Southeast Asian tropical rainforests, where the species diversity of trees is extremely high (Ashton 2005). Here we briefly describe our current research on insect seed predators and future research plans.

"General reproduction" endemic to Southeast Asian tropical rainforests

Although seeds are superior food resources for insects in terms of nutrition, almost no plants produce seeds constantly. Therefore, the reproductive phenology of a host plant is crucial to its insect seed predators.

In Southeast Asian tropical rainforests, many trees, herbs and lianas belonging to various families in a community flower synchronously at irregular intervals of 2-10 years (Ashton et al. 1988; Appanah 1993; Sakai et al. 2006). The phenomenon is called "general flowering" (Ashton et al. 1988; Appanah 1993), and usually lasts three to six months (Sakai et al. 1999, 2006). Following the flowering period, the trees fruit synchronously and subsequently disperse the seeds.

We define "general reproduction (GR)" here as the series of such community-level phenomena consisting of general flowering, subsequent fruiting, and seed dispersal. There are a lot of seeds near the end of a GR period, whereas there are a considerably smaller number of seeds during non-GR periods compared with the latter half of GR periods.

So far, many studies have addressed factors affecting the evolution of GR and attempted to answer the question of why many plants in a community synchronously flower at supra-annual and irregular intervals (e.g., Ashton et al. 1988; Kelly 1994; Curran et al. 1999; Brearley et al. 2007; Hosaka et al. 2011).

Predator satiation hypothesis

The predator satiation hypothesis is one of the hypotheses to explain the ultimate factors promoting the evolution of GR (Kelly 1994; Sun et al. 2007; Hosaka et al. 2011). The hypothesis takes into account three phenomena that enable plants to lower seed predation levels and raise seed survival rates: (1) a long-term non-fruiting period between two successive GR periods, which imposes high mortality on seed predators; (2) mass production of seeds at the community level over a short time, which satiates seed predators; and (3) unpredictable, irregular intervals between two successive GR periods, which prevent seed predators from adjusting their life cycles to periods of seed production via dormancy or migration. Although this hypothesis is the most strongly supported explanation for synchronous reproduction in many plant species in temperate regions (Kelly 1994), only a few investigations have provided empirical evidence that supports this hypothesis as an explanation of the ultimate factors of the evolution of GR. In order to test the validity of this hypothesis for GR evolution, it is necessary to determine the life history, host range and spatio-temporal variation in the abundances of individual species of insect predators in relation to the availability of their host seeds during both GR and non-GR periods.

Major insect seed predators occurring during GR

So far, most previous studies on insect seed predators occurring during GR have focused on those feeding on seeds of dipterocarp trees, most of which flower (reproduce) only during GR periods (Fig. 1).

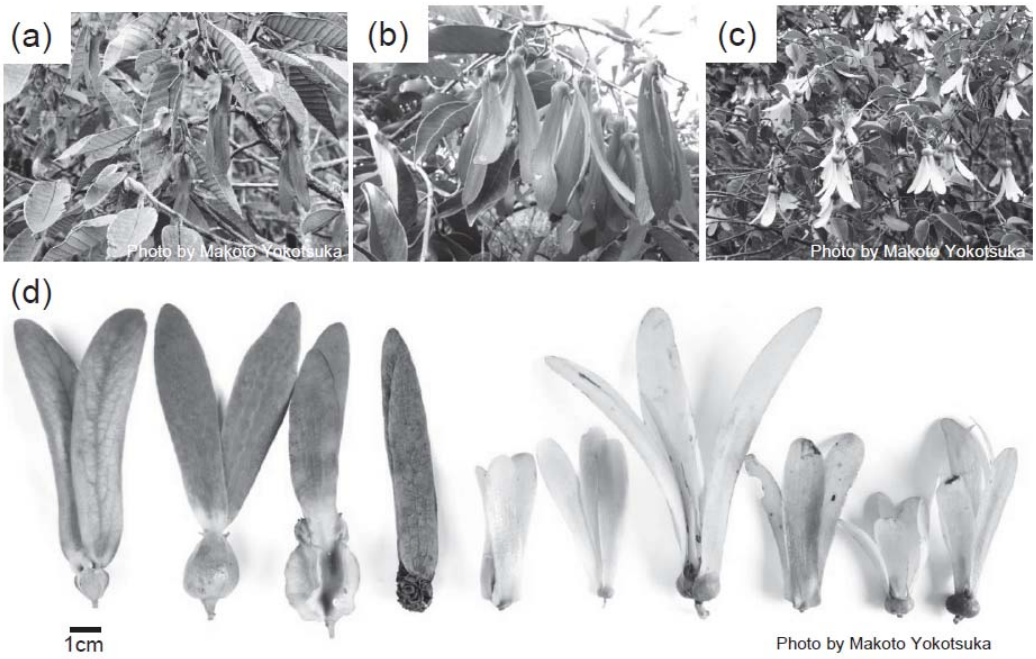

Fig. 1 Fruits of dipterocarp tree species that reproduce during general reproduction periods: pre-dispersal maturing fruits of *Dipterocarpus stellatus* (a), those of *Shorea beccariana* (b), those of *Dryobalanops aromatica* (c), and post-dispersal fruits of ten dipterocarp species (d), *Dip. geniculatus*, *Dip. globosus*, *Dip. stellatus*, *Dip. pachyphyllus*, *S. acuta*, *S. bullata*, *S. beccariana*, *S. macroptera*, *Dry. aromatica*, and *Dry. lanceolata* (from left).

Dipterocarp seeds are known to be attacked mainly by weevils (Curculionoidea; Coleoptera, Fig. 2a, b, c, d), bark beetles (Scolytidae; Coleoptera, Fig. 2e), and small moths (Tortricidae, Pyralidae etc.; Lepidoptera, Fig. 2f, g, h) (Curran and Leighton 2000; Lyal and Curran 2000; Nakagawa et al. 2003; Sun et al. 2007; Hosaka et al. 2009, 2011; Fig. 2). In weevils and most small moths, an adult lays an egg on each pre-dispersal fruit in the canopy (Asano, unpublished data). In most of these species, larvae feed on the fruits/seeds from the inside and pupate inside the fruits (Fig. 3a, b, e, f). In contrast, in most bark beetles, adults lay eggs on dispersed fruits on the ground (Asano, unpublished data). Generally, an adult bark beetle lays 10 to 30 eggs inside a fruit after it perforates the fruit with its mandible (Fig. 3c, d). In some species, larvae might also feed on fungi occurring inside the fruits in addition to the fruit bodies, or might feed only on fungi occurring inside the fruits (Farrell et al. 2001).

Previous studies on insect seed predators associated with GR

Lyal and Curran (2000) investigated the host ranges of *Alcidodes* (Curculionidae; Coleoptera), which is one of the weevil genera including some dipterocarp seed predators, by sampling seeds of 70 species of five genera in Dipterocarpaceae in South and Southeast Asia. Although the specificity of the host range of insect seed predators had been assumed to be rather high in the tropics, they found that the host-specificity of *Alcidodes* species is not as high as previously assumed. However, the host range of each of the *Alcidodes* species is limited within the family Dipterocarpaceae.

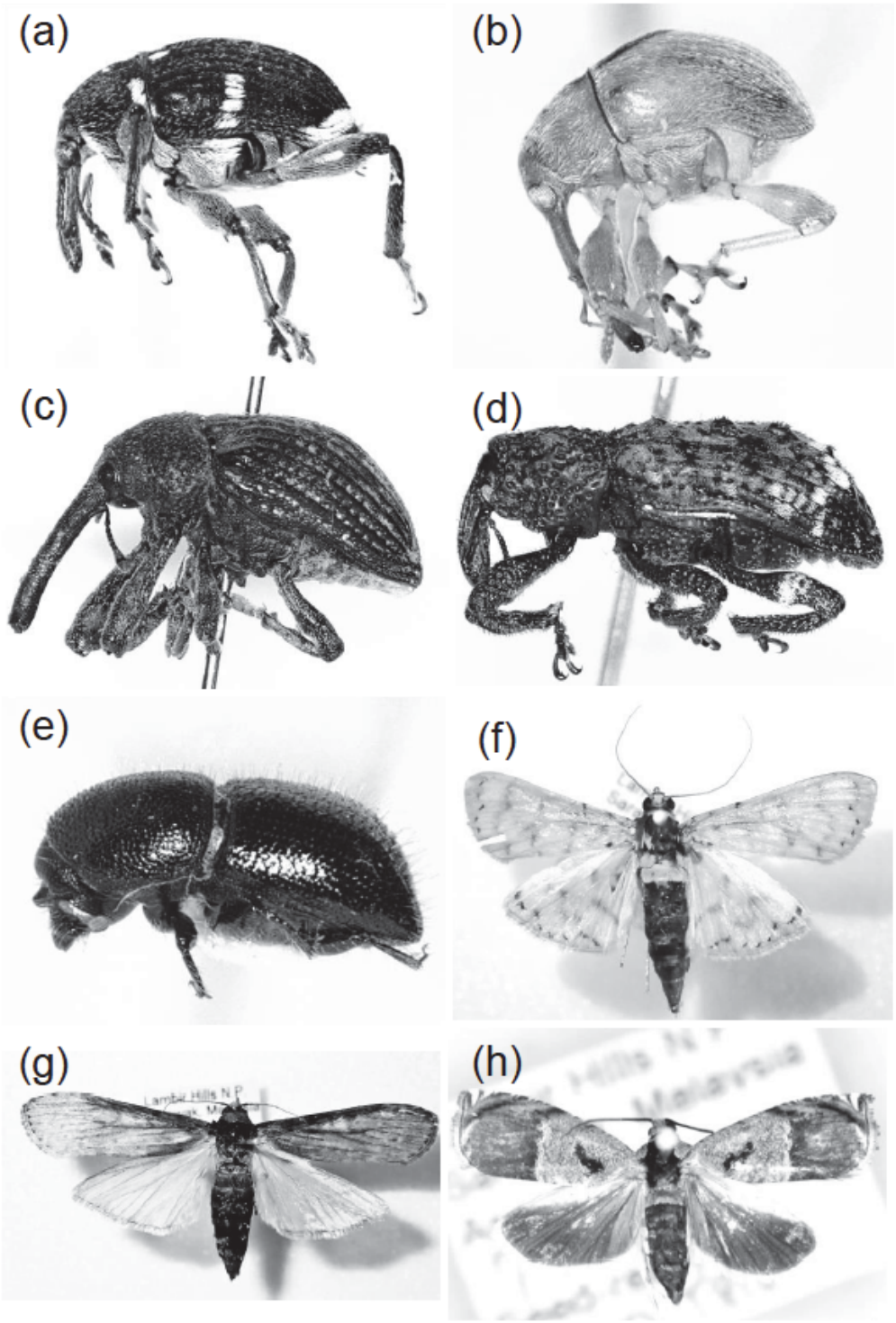

Fig. 2 Insect seed predators that emerged from dipterocarp seeds: two weevil species belonging to Nanophyidae, *Damnux* sp. (a) and *Nanophyes* sp. (b), two weevil species belonging to Curculionidae, *Alcidodes* sp. (c) and *Niphades* sp. (d), a bark beetle species, *Coccotrypes* sp. (e), a Crambidae moth species (f), and two tortricid moth species belonging to Olethreutinae, a genus-unknown species (g) and a *Andrioplecta* sp. (h).

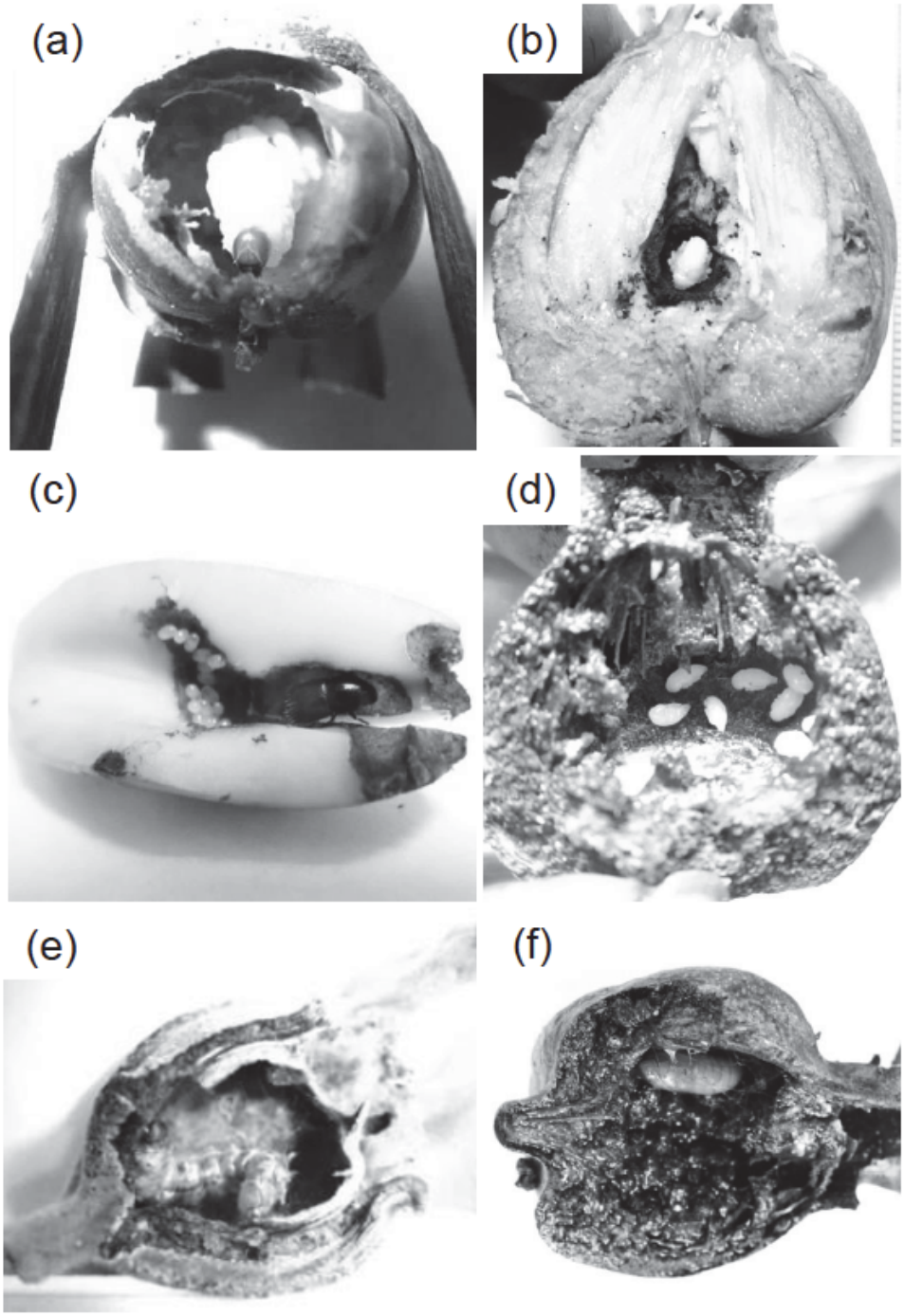

Fig. 3 Insect seed predators inside dipterocarp seeds: a larva of a weevil inside a *Dryobalanops lanceolata* fruit (a), a pupa of a weevil inside a *Dipterocarpus globosus* fruit (b), an adult of bark beetle laying eggs inside a fruit of *Shorea* sp. (c), pupae of a bark beetle inside a fruit of *Dip. globosus* (d), a larva of a small moth inside a *Dip. geniculatus* fruit (e), and a pupa of a small moth inside a *Dip. globosus* fruit (f).

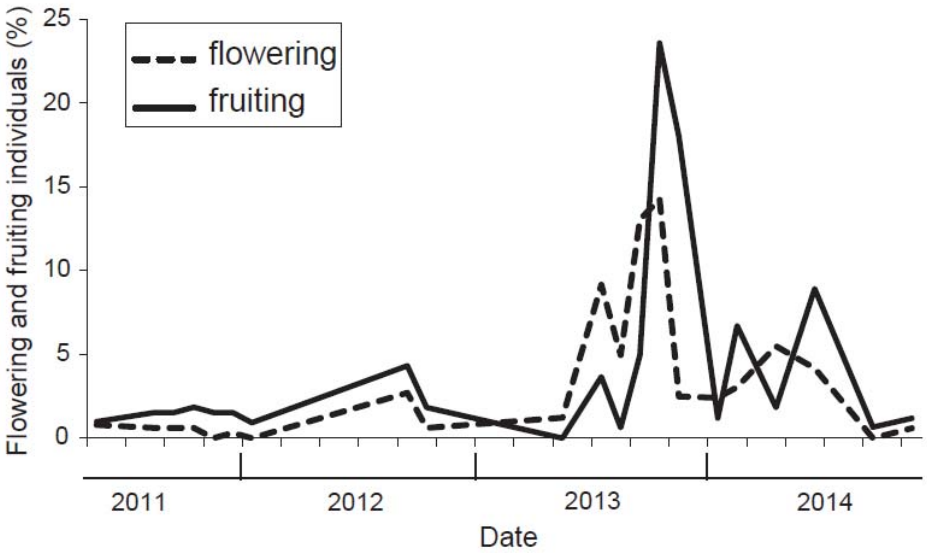

Fig. 4 Reproductive phenology of plants in the canopy of tropical rainforest at Lambir Hills National Park, Sarawak. The percentages of flowering and fruiting individuals in all of the plants that were the targets of our monthly census from April 2011 to October 2014 (Itioka et al. *unpublished data*) are shown. The number of target plants, including trees, lianas and epiphytes, was at least 300 of c. 180 species until January 2012, and thereafter 178 of 64 species.

Nakagawa et al. (2003) investigated insect seed predators of 24 dipterocarp species in a Bornean lowland forest (Lambir Hills National Park, Miri) during the two GR periods in 1996 and 1998. They found 51 species of insect seed predators, including 18 undescribed species. In addition, they showed that the host ranges of the insect seed predators that appeared in these GR periods changed between the two GR periods.

Nakagawa et al. (2005) described the patterns of seed survivorship with mortality due to predations by insects and vertebrates on six dipterocarp species during the GR period in 2001–2002 at the same site as studied in Nakagawa et al. (2003). They demonstrated that the seeds suffered predation by insects at their various growth stages from the stage of ovule in the ovary through the post-dispersal stage, and that insects imposed severer damage on dipterocarp seeds than the vertebrate predation.

Based on insect seed predators collected from seeds of 11 *Shorea* (Dipterocarpaceae) species during the GR occurring two years in a row in Pasoh Forest Reserve in Malay Peninsula, Hosaka et al. (2009) reported that four weevil species and one tortricid moth species dominated the assemblage of seed predators feeding on GR-participating *Shorea* species, that the predator species composition changed along the seed maturation process, and that most of the predators preyed on seeds of several tree species. In addition, the predation rate was higher in the second GR than in the first GR of the two consecutive GR events (Hosaka et al. 2011).

Our current study

We have been studying insect seed predators feeding on dipterocarp seeds at Lambir Hills National

Park (LHNP), Miri, Sarawak (4°20'N 113°50'E; altitude 150–250 m) since 1996. Although GR usually occurs at intervals of 2-10 years (Ashton et al. 1988; Appanah 1993; Sakai et al. 2006), two GR events occurred during the two consecutive years from June 2013 to January 2014 (here we call this event "GR-13") and from April to October 2014 (here we call the second event "GR-14") (Fig. 4). In these last two GR periods, we sampled seeds of 36 dipterocarp species and 57 non-dipterocarp species and collected insect seed predators by rearing both pre- and post-dispersal seeds that we sampled.

Based on the samples of five dipterocarp species during these two consecutive GR events, we have performed a few analyses on the difference in levels of insect seed predation between the two GR periods. The preliminary results showed that the percentages of insect seed predation were higher in GR-14 than in GR-13 for almost all dipterocarp species, suggesting that the results support a prediction arising from the predator satiation hypothesis. After fully analyzing the data, we are planning to publish the results in a journal soon.

Our future research plans

Most of the previous studies on insect seed predators placed the main focuses on seed predation of dipterocarp seeds during GR periods, as described above. However, the following questions also still remain unanswered: whether the species composition of insect seed predators is stable and predictable across GR events or not, how insects preying on abundant seeds during GR periods survive lack of seeds during non-GR periods, and what insects prey on non-dipterocarp seeds.

In order to answer these questions, we have started to routinely sample seeds of all tree species in a few fixed plots and routes in LHNP, and started to preliminarily analyze a part of the data from the already obtained samples. Moreover, we have been conducting several types of experimental rearing of insect seed predators in both the laboratory and field since April 2015.

Through these activities, we have obtained data on the difference in species composition of insect seed predators among GR events, and data on the diversity of insect seed predators, probably including many undescribed species, that feed on non-dipterocarp seeds. In addition, from the preliminary analyses, we have got results suggesting that at least several weevils preying on dipterocarp seeds during GR periods are able to diapause, and that various of these weevils emerged from non-dipterocarp seeds.

There are still a lot of other interesting questions to be answered about the biology and ecology of insect seed predators in Southeast Asian tropical rainforests. For getting the answers, we will need to continue the routine census on a long-term basis at fixed points such as LHNP.

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