Patterns of dipterocarp seed utilization by insect seed predators in a Bornean tropical rain forest

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Summary

Chapter 1. General introduction

Diverse species from various insect taxa use seeds of plants as their main food resources. Seeds are preferable food resources for many insects from a standpoint of nutrition values. However, seeds are also burdensome food resources to utilize as main foods for the insects, because the seeds of most plant species are available only during limited periods and because they are usually protected by the diverse chemical and physical mechanisms that individual plant species have developed in their own ways. How seed-eating insects have adapted their feeding traits to the limited availability and the anti-herbivore defenses is one of the most interesting subjects in the evolutionary biology and ecology of interspecific interactions between seed predators and seeds.

Many species of canopy trees in the lowland tropical rainforests of Southeast Asia synchronously reproduce at the community level at irregular intervals of 2–10 years. Such reproductive periods are termed "community-wide synchronized reproduction" (hereafter abbreviated as CSR) in this study. Dipterocarpaceae is a dominant family that comprises many canopy tree species in the lowland tropical rainforests of Southeast Asia. Most dipterocarp species in the region produce large fruits only during CSR periods. To date, various insect seed predators, including many species of weevils, bark beetles, and small moths, have been shown to prey on dipterocarp seeds. However, few studies have not attempted to elucidate in depth the patterns of seed utilization by the insect seed predators in the tropical rainforest areas. Therefore, to better understand how the seed-eating insects utilize the dipterocarp seeds that are supplied supra-annually at irregular intervals, I investigated the spatially and temporally dynamic patterns of the dipterocarp seed

utilization by seed-eating insects in a Bornean lowland dipterocarp forest.

Chapter 2. Study site and Materials

The study site was a primary lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20'N, 113°50'E; altitude, 50–250 m). The mean annual temperature and precipitation were 26°C and 2,600 mm, respectively. The forest at the study site is composed of more than 1,100 tree species belonging to approximately 80 families, more than 20% of which reproduce during CSR periods. Most plant species that reproduce during CSR periods, including most of the dipterocarp species in that region, produce seeds only during CSR periods.

All of my research works in the study site were conducted from September 2013 to January 2014 and from April to October 2014. During the study period, there was a CSR event that lasted approximately 15 months from July 2013 to October 2014.

Dipterocarpaceae is one of the dominant tree families in the lowland tropical rainforests of Southeast Asia. Many dipterocarp species in the region only reproduce during CSR periods. The fruits of Dipterocarpaceae are “nut”. The seeds are enveloped in hard pericarps. The seeds of dipterocarp species are preyed on by weevils, bark beetles, and small moths. The dominant seed-eating weevils are *Damnux* spp., *Merregallia* spp. and *Nanophyes* spp. belonging to Nanophyinae (Brentidae), and *Alcidodes* spp. and *Niphades* spp. belonging to Curculioninae (Curculionidae). The bark beetle species are *Coccotrypes* spp. belonging to Scolytinae (Curculionidae). Most small moths preying on the seeds of dipterocarp species belonged to the Tortricidae or Pyralidae.

Chapter 3. Differences in the fruit maturation stages at which oviposition occurs among insect seed predators

In this chapter, I aimed to determine the timings of attacking seeds/fruits in insect seed predators feeding on five dipterocarp species, *Dipterocarpus globosus, Dryobalanops aromatica, Shorea beccariana, S. acuta* and *S. curtisii,* which reproduced during the same period. I investigated the occurrence frequencies of the insect seed predators at various growth stages by collecting both un-fallen and fallen fruits at several times as the seeds/fruits were getting matured from September to December 2013.

Dominant insect seed predators of the five tree species were weevils and bark beetles;

one or two congeneric weevil species preyed on seeds of each of the five tree species, and one bark beetle species, *Coccotrypes gedeanus,* preyed on seeds of all of the five tree species. Many larvae at relatively elder growth stages in each weevil species were found in pre-dispersed (un-fallen) fruits, while almost all bark beetles at various growth stages were found in post-dispersed (fallen) fruits. These results suggested that, among the dominant insect seed predators of the five dipterocarp species, the weevil species oviposit on the pre-dispersed fruits and start their larval growth before seed dispersal, while the bark beetle species oviposit, and its larvae start to grow, in the post-dispersed fruits.

Chapter 4. Host range of a seed-eating bark beetle, *Coccotrypes gedeanus* (Col.: Curculionidae: Scolytinae)

In this chapter, the host preference and host range of *C. gedeanus* was determined by sampling 22,216 fruits from 137 species of 59 genera belonging to 24 families. *Coccotrypes gedeanus* adults were found in the fruits of 51 species from 19 genera belonging to 13 families, and were observed to settle in the fruits of 34 species of 11 genera belonging to 6 families to initiate breeding. Except one plant species, the rest of the 34 plant species were confirmed to bear “nut” or “drupe” type fruit. These results suggested that a population of *C. gedeanus* utilize seeds of various plant species simultaneously. The polyphagy of the bark beetle might be adaptive for survival in the Bornean tropical rain forests where the density of each plant species is low, and most plants produce fruits at unpredictably long intervals. My results also suggested that the characteristics of fruit might affect the host plant preference of *C. gedeanus* adults and/or the growth performance of *C. gedeanus* larvae.

Chapter 5. Host ranges of seed-eating weevils in dipterocarp fruits

In this chapter, I aimed to examine the host ranges of seed-eating weevils feeding on dipterocarp fruits during the CSR period. In total, I collected 22,322 fruits from 44 species of six dipterocarp genera and got 487 adult weevils by rearing the sampled fruits. It was revealed by the identification to species based on their morphological characteristics that the adult weevils comprised 30 species of seven genera belonging to two families.

Except for *Alcidodes toyi* and *Niphades* sp. 1, each weevil species fed on the seeds of one or more species in a single genus. Although the host range of each of the three

following genera, *Alcidodes, Niphades* and *Ctenomerus*-like genus, covered two or more dipterocarp genera, that of each of the other four genera, was limited to a single genus: *Nanophyes* fed only on *Shorea* fruits and the other three, *Mellegallia*, *Damnux* and *Corponinus*-like genus, fed only on *Dipterocarpus* fruits. These results suggest that the host ranges of most dipterocarp-eating weevil species, and those of some weevil genera, are limited to a particular plant genus.

To confirm the correctness of my morphological identification in a part of *Alcidodes* species, I decoded the sequences of the mitochondrial COI gene of sampled 23 individuals comprising seven morphological species. The results suggest that *A. toyi*, *A. hoptomachus* and *A. curranae* are included within the range of one species and that the morphological identification is difficult to distinguish *A. humeralis* individuals from small individuals of *A. toyi* group.

Chapter 6. Seed predation in the two fruiting events during an exceptionally long period of community-wide synchronized reproduction

Seed predation is a key factor in understanding the ecological and evolutionary factors affecting CSR. Masting, which is the intermittent production of enormous seeds by a population of plants, is proposed to decrease seed mortality due to predation in two ways: by depressing predator abundance through extended and unpredictable absences of seeds; and by satiating predators via mass seed production (predator satiation hypothesis). If the hypothesis is also valid in CSR, the incidence of seed predation will be higher in a fruiting event that occurs soon after a previous fruiting event, because the intervening period of seed absence would be inadequate to starve the predators. In this chapter, I examined seed predation by insects, focusing on five dipterocarp species that exceptionally reproduced twice during an extended CSR period.

All of the five species suffered more intense seed predation in the second fruiting event, consistent with the prediction expected from the predator satiation hypothesis. Weevils, bark beetles and mammals were the main cause of increased seed predation in three, one and one plant species, respectively. However, seed predation intensity did not increase during the second fruiting event in a few combinations of predator and plant species. I discuss the possibility that competition for seeds among predators and/or the interspecific differences in life history traits among predators might affect the varying

intensities of seed predation among dipterocarp species by different seed predators.

Chapter 7. General discussion

In this thesis, I aimed to increase ecological data and information necessary for elucidating the resource partitioning in assemblages of seed-eating insects in the Southeast Asian tropical rainforest by empirically investigating the ecological characteristics of seed-eating insects on the dipterocarp seeds in a Bornean primary lowland forest during a CSR period.

The results shown in the preceding three chapters (Chapter 3, 4 and 5) indicate that the patterns of dipterocarp seed utilization differ between the bark beetles and the weevils; the bark beetles start their life cycles in fallen fruits of various plant species, while almost all of the weevil species start their life cycles in un-fallen fruits of a particular dipterocarp genus. The results suggest that the weevils and the bark beetles that feeding on dipterocarp seeds share the food resources (seeds) by having different seed utilization patterns in each insect species. A plausible factor that affects the difference in seed utilization patterns among the insect seed predators is considered to be the chemical defenses of seeds against seed predators.

Although the predator satiation hypothesis is considered to be the most reasonable hypothesis that explains the factors promoting the evolution of CSR, there have not been enough empirical studies. The results of Chapter 6 that the intensity of seed predation by several insect seed predators increased in the fruiting event that occurred soon after the previous fruiting event. In addition, the results of Chapter 4 suggest that a seed-eating bark beetle *C. gedeanus* could have a negative effect on the reproduction of a wide range of plant species. These results suggest that a long period of seed absence is effective to decrease the seed mortality due to seed predation by a part of the insect seed predators feeding on dipterocarp seeds during the following CSR period in at least four dipterocarp species and the highly polyphagy as observed in *C. gedeanus* is presumed to increase the effects of community-level synchronization in satiating dominant generalist seed predators and to consequently promotes the evolution of CSR.

The biology of the seed-eating insects on dipterocarp seeds during CSR periods has gradually become clear. For better understanding the patterns of resource utilization among the assemblage of insect seed predators in the Southeast Asian tropics, the biology

and ecology of insect seed predators feeding on various plant species of multiple families are required to be studied during both CSR-periods and non-CSR periods.