High degree of polyphagy in a seed-eating bark beetle, *Coccotrypes gedeanus* (Coleoptera: Curculionidae: Scolytinae), during a community-wide fruiting event in a Bornean tropical rainforest

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ABSTRACT A bark beetle *Coccotrypes gedeanus* Eggers (Coleoptera: Curculionidae: Scolytinae) is a dominant insect seed predator of dipterocarp fruits in the lowland tropical rainforests of Southeast Asia. In this study, 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 in a primary lowland mixed dipterocarp forest in Borneo. *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 rainforests where the density of each plant species is low, and most plants produce fruits at unpredictably long intervals. Our 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.

Key words: Dipterocarpaceae, general flowering, masting, predator satiation hypothesis, Southeast Asian tropical rainforests

INTRODUCTION

In the lowland tropical rainforests of Southeast Asia, Dipterocarpaceae is a dominant family that includes many canopy tree species (Ashton 2004; Ghazoul 2016). Most dipterocarp species in the region produce large fruit at irregular intervals of 2–10 years, synchronously with many other tree species at the community level (Appanah 1985; Ashton et al. 1988; Sakai et al. 1999, 2006). Such reproduction periods are termed "community-wide synchronized reproduction" (CSR), and start with community-wide flowering, which was originally termed "general flowering". *Coccotrypes gedeanus* Eggers (Coleoptera: Curculionidae: Scolytinae) is a bark beetle and one of the most dominant insect predators of dipterocarp seeds. This beetle reproduces during CSR periods in a Bornean lowland tropical rainforest (Nakagawa et al. 2003; Iku et al. 2018), and is thus predicted to affect the success of dipterocarp reproduction. However, limited biological information on *C. gedeanus* is available.

Many *Coccotrypes* species breed in small hard seeds (Kirkendall et al. 2015), most are considered to have wide host ranges (Wood & Bright 1992), and some can use seeds as well as bark, leafstalks, and other plant tissues as their breeding spaces (Jordal et al. 2002, Kirkendall et al. 2015). Although several studies have reported that *C. gedeanus* uses the seeds and leafstalks of multiple plant families as host plants (Beaver 1979a; Wood & Bright 1992; Jordal et al. 2002, Nakagawa et al. 2003), most studies have been based on fragmentary records and have included insufficient seed samples obtained by routine sampling from a site. Thus, to date, the host preference and host range of *C. gedeanus* at the population level have not been sufficiently elucidated.

In this study, to determine the host preference and host range of *C. gedeanus*, we repeatedly sampled fruits of
various tree species and collected bark beetles from the sampled fruits during a CSR period in a Bornean tropical rainforest.

MATERIALS AND METHODS

Study site

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 (Kume et al. 2011). The forest at the study site is composed of more than 1,100 tree species belonging to approximately 80 families (Lee et al. 2002), more than 20% of which reproduce during CSR periods (Sakai et al. 2006). Most plant species that reproduce during CSR periods, including most of the dipterocarp species in that region, produce seeds only during CSR periods.

The field survey was conducted in two research plots (an 8 ha plot: 200 × 400 m and a 4 ha plot: 200 × 200 m) and three belt transects along sightseeing trails (approximately 10 m × 1 km, 10 m × 1 km, 10 m × 2 km, respectively). Almost all trees over 10 cm DBH in the research plots, consisting of approximately 6,100 and 2,800 trees in the 8 and 4 ha plots, respectively, were identified at the species level. Although most trees in the belt transects were not identified, the species composition of the trees was similar to that within the two research plots.

Sample collection

Fruit was collected in the study site over 9 months in a long CSR period from August 2013 to October 2014 (see Iku et al. 2017 for details). We repeatedly collected the fallen fruits of various plant species within the two research plots.

Coccotrypes gedeanus

*Coccotrypes gedeanus* is a bark beetle species and a seed predator in a wide area of Southeast Asia (Fig. 1a) (Wood & Bright 1992). One or a few female adults burrow into a post-dispersal fruit of the host species, excavate tunnels and galleries inside the fruit, including the seed part, and lay multiple eggs in the galleries. The larvae feed mainly on seed parts of the host fruit and pupate within the galleries (Fig. 1b) (Hulcr et al. 2007; Iku et al. 2018). After sib-mating, the new female adults disperse from the host fruit (Jordal et al. 2002). Usually, more than 15 new adults appear from a host fruit, which has lost its germination capacity.

Wood & Bright (1992) reported that the beetle used seeds of plants belonging to Anacardiaceae, Burseraceae, Dipterocarpaceae, and Moraceae as its food resources, although it is unclear whether the predation occurred during CSR periods. In the study site, the beetle was confirmed to prey on seeds of plants belonging to mainly Dipterocarpaceae, but also Celastraceae, Moraceae, and Myrtaceae during a CSR period (Nakagawa et al. 2003). The beetle usually utilizes plant seeds as its food resources; however, in some cases, such as an absence of plant seeds around its habitats, it apparently also uses leafstalks (Beaver 1979a).
plots and the three belt transects, mainly targeting canopy tree species, at intervals of 1–3 weeks during the CSR period. Fifty fruits were collected from each species per sampling event. When the total number of fallen fruits was less than 50, we collected as many as possible. We dissected the sampled fruits to detect any bark beetles inside. We also recorded the presence or absence of bark beetle eggs or larvae in a small fraction of sampled fruits per plant species. The plant species where at least one *C. gedeanus* adult was found with their eggs or larvae in a fruit, we considered that the bark beetle could have settled in the fruit of the plant species and started breeding. All sampled bark beetles were preserved in 99.5% ethanol soon after sampling.

**Identification of the collected bark beetles**

We sorted *C. gedeanus* from all collected bark beetles based on their morphological characteristics. Bark beetle species belonging to *Coccotrypes* are often difficult to distinguish based on morphological characteristics alone (Jordal et al. 2002; Hulcr et al. 2015); therefore, we also used DNA barcoding (Hebert et al. 2003) to confirm the identification based on morphological characteristics. Identification via DNA barcoding is based on the sequences of the mitochondrial cytochrome oxidase subunit I (COI) gene, which is a standard marker used to detect within- and among-species variations in bark beetles (Jordal et al. 2002; Hulcr et al. 2015).

From the collected bark beetles that shared a host plant species and were classified as *C. gedeanus* according to their morphologies, we haphazardly sampled one to three individuals for DNA-barcoding. We extracted genomic DNA from one to four legs of each sampled beetle using a NucleoSpin Tissue Kit (Macherey-Nagel, Düren, Germany) according to the manufacturer’s protocol, except that the volume of Buffer BE was adjusted to 10 µL. Polymerase chain reaction (PCR) was used to amplify the COI region with standard primers used for DNA barcoding (LCO1490 and HCO2198: Folmer et al. 1994) and Ex Taq DNA polymerase (TaKaRa, Kusatsu, Japan). The PCR program was as follows: 94°C for 5 min, followed by 30 cycles of 94°C for 30 s, 50°C for 30 s, and 72°C for 1 min, and a final extension at 72°C for 7 min. The PCR products were purified using ExoSAP-IT (Affymetrix, Santa Clara, USA), and then sequenced using a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, USA) and a Genetic Analyzer 3130xl (Applied Biosystems).

We compared the 378 bp COI sequences of the sampled bark beetles to that of *C. gedeanus* registered in GenBank (accession number AF375310). If a sampled beetle shared 99% identity with the registered sequence, the sampled beetle was identified as *C. gedeanus*.

**RESULTS**

In total, we collected 22,216 fruits from 137 species of 59 genera belonging to 24 families (Table 1). The total number of adult bark beetles obtained from the collected fruit was 3,710. Of these, 1,791 were *C. gedeanus*, which were collected from 51 species belonging to 19 genera of 13 plant families (Table 1). There were no inconsistencies between identification based on morphological characteristics and that based on sequences of the COI gene. In each of 34 species belonging to 11 genera of six families, at least one *C. gedeanus* adult settled in fruits to begin breeding (Table 1). Except Allantospermum borneense (Irvingiaceae), all plant species were confirmed to bear nut- or drupe-type fruit (Table 1).

Bark beetles other than *C. gedeanus* accounted for approximately 51.7% of those obtained from fruits. All belonged to *Coccotrypes*, comprising at least six species; however, they could not be identified at the species level.

**DISCUSSION**

The results of this study strongly suggest that *C. gedeanus* possesses a high degree of polyphagy, at least during CSR-periods; the bark beetle settled in seeds of various plant species spread over a broad taxonomic range, including at least six families belonging to five orders (Table 1). Previous studies on seed-eating weevils and moths in the tropics showed that most insect seed predator species had a much narrower range of host plants than *C. gedeanus* (Janzen 1980; Hopkins 1983; Lyal & Curan 2000; Nakagawa et al. 2003; Hosaka et al. 2009): among insect seed predator species whose host plant ranges were determined, more than 80% used host plants within the range of a single genus, more than 90% used those within the range of a single family, and only a few (<7%) used those belonging to multiple families (up to a maximum of five per insect predator species). These findings demonstrated that *C. gedeanus* has a notably wider host range compared with other seed-eating insects.

In addition to previous studies based on fragmental observations (Beaver 1979a; Wood & Bright 1992; Jordal et al. 2002, Nakagawa et al. 2003), this study presents evidence that a population of this bark beetle species
Table 1. Total number of sampled fruits, total numbers of collected adult individuals of *Coccotrypes gedeanus* and other bark beetles, and mean diameter of sampled fruits and fruit type, for each plant species. Data in a line and in boldface indicate the plant species where at least one *C. gedeanus* adult was observed to settle in fruits.

| Host plant | No. of fruits | No. of *C. gedeanus* | No. of other bark beetles | Mean diameter of fruits ± SD | Fruit type* |
|------------|---------------|----------------------|----------------------------|-------------------------------|-------------|
| Actinidiaceae |               |                      |                            |                               |             |
| *Saurauia* sp. 1 | 20       | 0                     | 0                          | 0.77 ± 0.07                   | B           |
| Anacardiaceae |               |                      |                            |                               |             |
| *Parishia maingayi*? | 49       | 4                     | 0                          | 0.76 ± 0.06                   | D           |
| *Swintonia acuta* Engl. | 260     | 19                    | 43                         | 0.70 ± 0.52                   | D           |
| *S. foxxworthyi* Elmer | 155      | 14                    | 24                         | 0.67 ± 0.28                   | D           |
| *Swintonia* sp. 1 | 425     | 5                     | 4                          | 0.60 ± 0.27                   | D           |
| *Swintonia* sp. 2 | 25       | 1                     | 2                          | 1.05 ± 0.37                   | D           |
| Annonaceae |               |                      |                            |                               |             |
| Genus unknown sp. 1 | 11       | 0                     | 0                          | 0.71 ± 0.09                   | D           |
| Burseraceae |               |                      |                            |                               |             |
| *Canarium* sp. 1 | 5        | 0                     | 0                          | 3.27 ± 0.16                   | D           |
| *Dacryodes macrocarpa* (King) H. J. Lam | 34       | 6                     | 28                         | 2.60 ± 0.31                   | D           |
| *Dacryodes* sp. 1 | 36       | 0                     | 0                          | 1.40 ± 0.10                   | D           |
| *Dacryodes* sp. 2 | 31       | 0                     | 0                          | 1.54 ± 0.09                   | D           |
| *Sanitaria mollis* Engl. | 87       | 0                     | 0                          | 1.47 ± 0.13                   | D           |
| *Sanitaria* sp. 1 | 113      | 0                     | 0                          | 1.26 ± 0.14                   | D           |
| *Scutinathe brumnea* Thwaites | 49       | 0                     | 0                          | 1.42 ± 0.15                   | D           |
| *Triomma malaccensis* Hook. f. | 17       | 0                     | 1                          | 1.08 ± 0.23                   | D           |
| Calophyllaceae |               |                      |                            |                               |             |
| *Calophyllum* sp. 1 | 84       | 7                     | 13                         | 1.37 ± 0.10                   | D           |
| Cardiopoteridaceae |         |                      |                            |                               |             |
| *Gonocaryum minus* Sleumer | 17       | 0                     | 0                          | 2.07 ± 0.14                   | D           |
| Diptercorpaceae |               |                      |                            |                               |             |
| *Anisoptera grossivenia* Slooten | 123      | 4                     | 1                          | 1.06 ± 0.14                   | N           |
| *Diptercorpus crinitus* Dyer | 401      | 3                     | 6                          | 1.08 ± 0.10                   | N           |
| *Dip. geniculatus* Vesque | 832      | 17                    | 23                         | 1.51 ± 0.69                   | N           |
| *Dip. globosus* Vesque | 936      | 363                   | 84                         | 2.06 ± 0.89                   | N           |
| *Dip. pachyphylus* Meijer | 810      | 0                     | 16                         | 1.55 ± 0.33                   | N           |
| *Dip. palembanicus* Slooten | 267      | 8                     | 27                         | 1.60 ± 0.92                   | N           |
| *Dip. stellatus* Vesque | 584      | 98                    | 54                         | 1.10 ± 0.51                   | N           |
| *Dip. tempehes* Slooten | 385      | 1                     | 24                         | 2.84 ± 0.91                   | N           |
| *Dryobalanops aromatica* Gaertn. | 2,184    | 96                    | 167                        | 2.20 ± 0.32                   | N           |
| *Dry. lanceolata* Burck | 1,637    | 137                   | 281                        | 1.57 ± 0.43                   | N           |
| *Hopea pterygota* P. S. Ashton | 2        | 0                     | 0                          | 1.21 ± 0.10                   | N           |
| *Hopea* sp. 1 | 157      | 0                     | 3                          | 0.94 ± 0.09                   | N           |
| *Shorea acuta* P. S. Ashton | 386      | 112                   | 56                         | 1.09 ± 0.37                   | N           |
| *S. beccariana* Burck | 2,088    | 585                   | 310                        | 2.12 ± 0.65                   | N           |
| *S. bullata* P. S. Ashton | 215      | 0                     | 0                          | 0.80 ± 0.51                   | N           |
| *S. confusa* P. S. Ashton | 277      | 0                     | 0                          | 1.21 ± 0.40                   | N           |
| *S. crassa* P. S. Ashton | 9        | 0                     | 1                          | 0.83 ± 0.12                   | N           |
| *S. curtisi* Dyer *ex* King | 208      | 40                    | 137                        | 0.72 ± 0.45                   | N           |
| *S. faguetiana* F. Heim | 562      | 5                     | 87                         | 0.81 ± 0.20                   | N           |
| *S. ferruginea*? | 217      | 25                    | 13                         | 1.07 ± 0.23                   | N           |
| *S. havilandii* Brandis | 32        | 2                     | 5                          | 1.21 ± 0.11                   | N           |
| *S inappendiculata*? | 213      | 36                    | 17                         | 1.31 ± 0.19                   | N           |
| *S. laxa* Slooten | 727      | 87                    | 35                         | 1.31 ± 0.39                   | N           |
| *S. macrophylla* (de Friese) P. S. Ashton | 4        | 3                     | 1                          | 2.86 ± 0.27                   | N           |
| *S. macroptera* Dyer | 482      | 26                    | 61                         | 0.95 ± 0.15                   | N           |
| *S. myriomeru* Symington *ex* P. S. Ashton | 15       | 0                     | 0                          | 0.64 ± 0.18                   | N           |
| *S. ovata* Dyer *ex* Brandis | 378      | 1                     | 99                         | 0.67 ± 0.27                   | N           |
| *S. parvifolia* Dyer | 379      | 1                     | 39                         | 0.75 ± 0.26                   | N           |
| *S. pilosa* P. S. Ashton | 6        | 1                     | 0                          | 1.89 ± 0.17                   | N           |
| *S. smithiana* Symington | 237      | 20                    | 44                         | 1.57 ± 0.44                   | N           |
| *S. superba* Symington | 554      | 2                     | 23                         | 0.76 ± 0.21                   | N           |
### Table 1. Continued.

| Host plant                        | No. of fruits | No. of *C. gedeanus* | No. of other bark beetles | Mean diameter of fruits ± SD | Fruit type<sup>1</sup> |
|-----------------------------------|---------------|----------------------|---------------------------|-------------------------------|-----------------------|
| *S. xanthophylla* Symington       | 147           | 1                    | 17                        | 1.56 ± 0.26                   | N                     |
| *Shorea sp. 1*                    | 19            | 1                    | 2                         | 2.04 ± 0.21                   | N                     |
| *Shorea sp. 2*                    | 333           | 15                   | 42                        | 1.32 ± 0.42                   | N                     |
| *Shorea sp. 3*                    | 3             | 2                    | 0                         | 2.91 ± 0.27                   | N                     |
| *Shorea sp. 4*                    | 5             | 0                    | 0                         | 1.09 ± 0.08                   | N                     |
| *Shorea sp. 5*                    | 8             | 0                    | 0                         | 0.47 ± 0.15                   | N                     |
| *Vatica badifolia P. S. Ashton*   | 54            | 0                    | 0                         | 0.56 ± 0.19                   | N                     |
| *V. micrantha* Slooten            | 825           | 1                    | 10                        | 0.39 ± 0.14                   | N                     |
| *V. nitens* King                  | 3             | 0                    | 0                         | 0.87 ± 0.09                   | N                     |
| *V. parvifolia P. S. Ashton*      | 556           | 3                    | 11                        | 0.51 ± 0.25                   | N                     |
| *V. umbonata?*                    | 20            | 6                    | 1                         | 2.76 ± 0.23                   | N                     |
| *Vatica sp. 1*                    | 46            | 0                    | 1                         | 0.46 ± 0.06                   | N                     |

**Ebenaceae**
- *Diospyros dictyoneura* Hieron ex Boerl. 69 0 0 1.18 ± 0.28 B
- *Diospyros sp. 1* 14 0 4 0.38 ± 0.07 B
- *Diospyros sp. 2* 2 0 0 1.08 B

**Euphorbiaceae**
- *Croton argyratus* Blume 5 0 0 1.76 ± 0.02 C
- *Macaranga bancana* (Miq.) Mull. Arg. 22 0 0 0.74 ± 0.14 C
- *Mac. gigantea* (Rechb. f. & Zoll.) Mull. Arg. 47 0 0 0.68 ± 0.09 C
- *Mac. trachypylly* Airy Shaw 48 0 0 0.75 ± 0.07 C
- *Mac. winkleri* Pax & K. Hoffm. 53 0 0 0.38 ± 0.03 C
- *Macaranga sp. 1* 65 0 0 0.54 ± 0.06 C
- *Malloctus eucatus* Airy Shaw 22 0 0 1.63 ± 0.15 C
- *Mal. leucodermites* Hook. f. 150 0 3 1.77 ± 0.15 C
- *Mal. penangensis* Mull. Arg. 17 0 0 1.60 ± 0.06 C
- *Malloctus? sp. 1* 56 0 0 1.43 ± 0.16 C
- *Malloctus? sp. 2* 66 1 1 1.13 ± 0.16 C
- *Malloctus? sp. 3* 55 0 0 1.18 ± 0.07 C
- *Malloctus? sp. 4* 4 0 0 1.77 ± 0.10 C
- *Malloctus? sp. 5* 25 0 0 0.94 ± 0.06 C
- *Malloctus? sp. 6* 53 0 0 1.08 ± 0.04 C
- *Psychopyxis glochiadifolia* Airy Shaw 16 0 3 1.37 ± 0.19 D or C

**Fabaceae**
- *Archidendron borneense* (Benth.) I. C. Nielsen 24 0 4 – L
- *Bauhinia sp. 1* 103 0 1 – L
- *Dialium inum L.* 30 0 2 2.59 ± 0.31 L
- *Koompassia malaccensis* Maingay 39 0 0 – L
- *Melletia? sp. 1* 28 0 1 – L
- *Sindora coriacea* (Baker) Prain 20 1 27 7.05 ± 0.66 L
- *Genus unknown sp. 1* 20 0 0 – L
- *Genus unknown sp. 2* 10 0 0 – L
- *Genus unknown sp. 3* 30 0 0 – L

**Fagaceae**
- *Lithocarpus leptogynus* (Korth.) Soepadmo 54 2 1 1.47 ± 0.10 N
- *Lithocarpus sp. 1* 103 7 6 2.62 ± 0.18 N
- *Lithocarpus sp. 2* 60 1 1 1.20 ± 0.10 N
- *Lithocarpus sp. 3* 37 0 0 2.85 ± 0.66 N
- *Lithocarpus sp. 4* 50 11 3 1.77 ± 0.14 N
- *Lithocarpus sp. 5* 15 0 0 1.72 ± 0.15 N
- *Lithocarpus sp. 6* 52 0 10 1.47 ± 0.12 N

**Irvingiaceae**
- *Allantospermum borneense* 63 1 0 2.01 ± 0.40 C
- *Allantospermum? sp. 1* 6 0 0 2.29 ± 0.10 C

**Lecythidaceae**
- *Barringtonia sp. 1* 89 5 24 1.47 ± 0.19 D

**Malvaceae**
- *Durio sp. 1* 82 0 0 0.91 ± 0.10 C
- *Heritiera sumatrana* (Miq.) Kosterm. 3 0 0 3.26 ± 0.22 SA
| Host plant | No. of fruits | No. of C. gedeanus | No. of other bark beetles | Mean diameter of fruits ± SD | Fruit type |
|------------|---------------|------------------|--------------------------|-------------------------------|------------|
| *Heritiera* sp. 1 | 53 | 0 | 0 | 1.17 ± 0.19 | SA |
| *Microcos* stylocarpa (Warb.) Burret | 16 | 0 | 0 | 1.50 ± 0.07 | D |
| *Pentace* corneri | 47 | 0 | 0 | 0.48 ± 0.07 | C or SA |
| *Pentace* sp. 1 | 45 | 0 | 1 | 0.37 ± 0.09 | C or SA |
| *Pentace* sp. 2 | 51 | 0 | 0 | 1.13 ± 0.21 | C or SA |
| *Pterocymbium* tubulatum (Masters) Pierre | 96 | 0 | 1 | 0.83 ± 0.05 | F |
| *Schoutenia* sp. 1 | 105 | 0 | 0 | 0.80 ± 0.09 | F |
| *Scaphium* macropodum Beunee ex K. Heyne | 27 | 0 | 0 | 0.28 ± 0.07 | F |
| *Scaphium* sp. 1 | 59 | 0 | 0 | 1.70 ± 0.19 | F |
| *Scaphium* sp. 2 | 108 | 1 | 0 | 0.54 ± 0.34 | F |
| Melastomataceae | | | | | |
| *Pternandra multiflora* Cogn. | 122 | 0 | 0 | 0.53 ± 0.10 | B |
| Moraceae | | | | | |
| *Artocarpus* anisophyllus Miq. | 1 | 1 | 3 | 8.20 | SY |
| *Artocarpus* sp. 1 | 9 | 0 | 0 | 4.22 ± 1.36 | SY |
| *Ficus* sp. 1 | 47 | 0 | 0 | 0.76 ± 0.07 | SY |
| *Ficus* sp. 2 | 31 | 0 | 0 | 1.06 ± 0.14 | SY |
| *Ficus* sp. 3 | 50 | 0 | 0 | 1.40 ± 0.09 | SY |
| *Ficus* sp. 4 | 31 | 0 | 0 | 1.85 ± 0.34 | SY |
| *Ficus* sp. 5 | 5 | 0 | 0 | 1.18 ± 0.03 | SY |
| *Ficus* sp. 6 | 17 | 0 | 0 | 2.24 ± 0.15 | SY |
| *Parartocarpus* venenous Becc. | 57 | 1 | 1 | 3.28 ± 2.01 | SY |
| Myrtaceae | | | | | |
| *Syzygium* sp. 1 | 13 | 0 | 0 | 2.11 ± 0.07 | B |
| *Syzygium* sp. 2 | 28 | 1 | 2 | 2.49 ± 0.32 | B |
| Peraceae | | | | | |
| *Chaetocarpus* castanocarpus Thwaites | 202 | 0 | 0 | 0.94 ± 0.20 | C |
| *Trigonopleura* malayana? | 57 | 0 | 1 | 0.96 ± 0.13 | D or C |
| Phyllanthaceae | | | | | |
| *Cleistanthus* sumatr anus (Miq.) Mull. Arg. | 2 | 0 | 0 | 1.67 ± 0.01 | C |
| Polygalaceae | | | | | |
| *Xanthophyllum* brevipes van der Meijden | 6 | 0 | 0 | 1.15 ± 0.12 | C |
| Primulaceae | | | | | |
| *Ardisia* macrophylla Reinw. ex Blume | 32 | 0 | 0 | 1.14 ± 0.14 | D |
| Putranjivaceae | | | | | |
| *Drypetes* sp. 1 | 74 | 0 | 0 | 1.02 ± 0.06 | D |
| *Drypetes* sp. 2 | 23 | 0 | 0 | 2.67 ± 0.29 | D |
| Rhamnaceae | | | | | |
| *Ventilago* malaccensis Ridl. | 112 | 0 | 0 | 0.12 ± 0.07 | SA |
| Rubiaceae | | | | | |
| *Mussaendopsis* beccariana Baill. | 53 | 0 | 0 | 0.46 ± 0.11 | B |
| Genus unknown sp. 1 | 5 | 0 | 0 | 4.18 ± 0.41 | B |
| Genus unknown sp. 2 | 2 | 0 | 1 | 0.82 | B |
| Sapotaceae | | | | | |
| *Madhuca* sp. 1 | 6 | 1 | 0 | 1.72 ± 0.15 | D |
| *Payena* endertii H. J. Lam | 113 | 0 | 2 | 0.87 ± 0.24 | D |
| *Payena*? sp. 1 | 26 | 0 | 0 | 1.06 ± 0.08 | D |
| Sapotaceae? | | | | | |
| Genus unknown sp. 1 | 34 | 0 | 2 | 1.64 ± 0.22 | D |

* D: Drupe, N: Nut, B: Berry, C: Capsule, L: Legume, SA: Samara, F: Follicle, SY: Syncarp.
High degree of polyphagy in a bark beetle Coccotrypes gedeanus might play a role in its survival. It is reasonable to infer that the high degree of polyphagy in C. gedeanus is adaptive for its survival in the Bornean tropical rain forests, where the density of each plant species is low and most of the plants produce fruit at unpredictably long intervals (Beaver 1979b, Novotny & Basset 2005). In addition, polyphagy helps to maintain the relatively abundant population of this bark beetle species in the assemblage of insect seed predators (Iku et al. 2017, 2018).

Our results also suggest that C. gedeanus could have a significant negative effect on the reproduction of a wide range of plant species due to damage on seeds through seed-feeding or burrowing by the adults, as well as due to seed predation by the larvae after the adults settle in the fruits (Table 1). The range of tree species that suffer such damage only by the adults is likely to be wider than that of tree species that suffer predation by the larvae. Therefore, it is possible that C. gedeanus might play a role in the evolution of CSR as one of key generalist seed predators according to the predator satiation hypothesis (Janzen 1974; Silvertown 1980; Kelly 1994), which explains the factors affecting CSR evolution. This hypothesis assumes that many plants have evolved to mast and synchronize their reproductive periods to reduce seed predation by sharing and satiating generalist seed predators (Janzen 1974; Sakai 2002). To date, vertebrate seed predators, most of which are highly polyphagous, have been considered such generalist predators (Janzen 1974). However, C. gedeanus, which was found to be a highly polyphagous insect seed predator in this study, is presumed to be a key predator that could impose seed predation pressure on a wide range of plant species to promote interspecific synchronization of their mast reproduction periods. To examine this hypothesis for C. gedeanus, temporal trends in population, seed abundance, host plant preference, and seed predation intensity on each plant species should be investigated over the long-term during both CSR and non-CSR periods.

In this study, although many C. gedeanus adults were observed to bore into fruits of various plant species, most of the fruits where C. gedeanus adults settled to breed were classified into nut- or drupe-type (Table 1). This suggests that fruit characteristics might affect host plant preference of C. gedeanus adults and/or the growth performance of C. gedeanus larvae. It is also possible that adults might visit the fruits to obtain nutrition from the fruits before oviposition. Additionally, they may not be able to settle in the fruits because of the thickness of flesh, the excessive moisture of flesh, and/or the toxicity of chemicals in seeds; it might take longer for the bark beetle adults to settle in other types of fruit than in the nut- or drupe-type fruits. These possibilities remain to be examined in future studies.

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