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Canopy crane survey of the hemipteran assemblage structure in a Bornean forest

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Abstract. Tropical forest canopies are home to an extremely high diversity of arthropods, but the abundance and community structures of species inhabiting tropical forest canopies remain unclear. We characterised assemblages of canopy-foraging hemipteran species, which are one of the most dominant groups in tropical forest canopies. We used a canopy crane to sample hemipteran assemblages in a Bornean rain forest from an average of 165 canopy trees per sample, over six sampling periods. Our sampling periods occurred during and after a community-wide synchronous flowering, called a general flowering (GF) event, which occur at irregular, supra-annual intervals in the region. During each sampling period, we assessed hemipteran abundance, species richness and species compositions. We also analysed correlations between GF events and tree families for the abundance and occurrence of the abundant hemipteran species. The results showed that the GF event caused dynamic changes in the species diversity and species compositions of adult hemipterans. We hypothesise that the availability of flowers, buds and seeds during a GF event influences assemblages of phytophagous hemipteran adults. In addition, the abundances of some opportunistic predaceous species were strongly correlated with the GF event, possibly due to increases in the abundance of prey that rely on floral resources, as well as plant materials. We found that specialisation of phytophagous species to the tree family level was uncommon in our study, with most species having more general occurrences and distributions. Our study highlights the usefulness of canopy cranes to characterise hemipteran assemblages in tropical forest canopies.

Key words. canopy arthropods, community structure, general flowering, herbivores, lowland dipterocarp forest, Southeast Asian tropics

INTRODUCTION

Tropical forest canopies are home to an extremely high diversity of arthropods. Since the late 1970s, many studies have examined insects in tropical forest canopies (Erwin, 1995; Basset, 2001a; Ozanne et al., 2003), but we still have little idea regarding the number of species, community structure, spatial or temporal distribution patterns and how canopy insects interact with other arthropods and plants (Novotny & Miller, 2014; Wardhaugh, 2014). Unveiling such patterns could reveal the structure of arthropod assemblages in tropical canopies as well as how such a high diversity of tropical arthropods can evolve and be maintained.

Canopy cranes allow detailed investigation of canopy arthropod assemblages. Arthropods are collected from the foliage of tree crowns by beating, sweeping and hand-collecting from the gondola of a canopy crane (Basset et al., 2003). Studies using canopy cranes in tropical forest canopies have revealed temporal variation in arthropod fauna (Kitching et al., 2007), interactions among insects and plants (Ødegaard, 2000, 2006), differences in herbivore communities among different tree species and groups (Basset, 2001b; Ødegaard, 2004), the distribution of arthropods in different microhabitats (Kitching et al., 2007; Wardhaugh et al., 2012; Wardhaugh, 2014), and species interactions between ants and spiders (Katayama et al., 2015).

One advantage of a canopy crane is the relatively easy access to many tree crowns within the diameter of the crane jib, allowing a more thorough assessment of the canopy community. Previous studies using canopy cranes have examined relatively large numbers of trees, i.e., more than 50 plants (Ødegaard, 2000, 2006; Katayama et al., 2015), and sought to clarify distribution patterns of arthropod assemblages. Other methods, such as fogging (Basset, 2001a), have targeted fewer than 20 trees (Moran & Southwood, 1982; Stork, 1987a, b; Adis et al., 1997; Davies et al., 1997; Floren & Linsenmair, 1997; Mawdsley & Stork, 1997; Wagner, 1997). Other canopy research methods, such as single-rope techniques, ladders, walkways and towers have similarly

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collected arthropods from only a handful of trees (Basset, 1997; Barone, 1998; Kishimoto-Yamada & Itioka, 2008). Because of the limited number of tree species examined using these methods, the species numbers of host-specific herbivores may be overestimated. Recent empirical studies have demonstrated that the proportion of host-specific species is lower than previously believed (e.g., Novotny et al., 2012; Kishimoto-Yamada et al., 2013).

Canopy cranes also allow temporal replication because of easy access and non-destructive survey methods. By contrast, fogging studies kill many arthropods in the entire tree and probably in adjacent parts of neighbouring trees, eliminating the possibility of re-sampling the same tree before re-colonisation by arthropods (Basset et al., 1997); thus, most fogging studies of tropical canopy arthropods have used only one or two censuses (e.g., Erwin, 1982; Stork, 1987a, b; Floren & Linsenmair, 1997; Guibert, 1997; Dial et al., 2006). Since beating, sweeping, and hand-collecting from the gondola of a canopy crane remove a relatively small fraction of the arthropods on the tree, the arthropods can recolonise relatively quickly. Consequently, canopy crane censuses can be conducted at regular intervals over a relatively long period (Basset, 2001b; Kitching et al., 2007; Wardhaugh et al., 2012; Wardhaugh, 2014; Katayama et al., 2015). Considering the dynamic changes in populations and species compositions that can occur in tropical insects (Wolda, 1978, 1983, 1992; Inoue et al., 1993; Kishimoto-Yamada et al., 2009), investigations of canopy arthropod assemblages need to include a temporal aspect in sampling.

Arthropods associated with flowers are likely to make up a large proportion of the canopy fauna and need to be considered when estimating the true diversity of canopy arthropods. A study of an Australian forest canopy showed that the density of arthropods on flowers can be significantly higher than on immature and mature leaves (Wardhaugh et al., 2012). In lowland dipterocarp rain forests in the Southeast Asian tropics, community-wide synchronous flowering events, called general flowering (GF), occur irregularly at intervals of several years (Appanah, 1985; Ashton et al., 1988; Sakai, 2002) and last from a few weeks to a few months (Ashton et al., 1988; Sakai, 2002). Most Dipterocarpaceae and many other canopy trees flower profusely during GF events and rarely flower between GF periods (Sakai et al., 1999a). GF events strongly influence insect populations that depend on floral resources, e.g., pollinators and pollen and flower feeders (Appanah & Chan, 1981; Kato et al., 2000; Itioka et al., 2001). Understanding canopy arthropod structure in Southeast Asian forests requires an examination of the effects of GF events on arthropod communities.

Hemiptera is the most diverse exopterygote order, with almost 100,000 described species (Gullan & Cranston, 2010), and is among the most abundant and species-rich canopy arthropod groups (Sutton & Hudson, 1980; Sutton et al., 1983; Stork, 1991; Moran et al., 1994; Guilbert, 1997). Hemipteran species include herbivores that feed on plant sap, predators, scavengers, necrophages, and a few hematophages (Hodkinson & Casson, 1991; Gullan & Cranston, 2010). In a Bornean rainforest, Itioka et al. (2003) showed that the abundance of the light-attracted Hemiptera assemblage increased during GF periods. This led us to hypothesize that GF events strongly affect the structure of hemipteran assemblages in the Bornean rainforest. However, no study has examined whether the increases in the abundances of some anthophilous hemipterans contribute to the increase in the overall species abundance, and whether the species composition of the hemipteran assemblage changes between non-GF and GF periods. In addition, the interactions between canopy plants and hemipteran species have never been investigated in detail in the Southeast Asian rainforest. In this study, we characterise patterns of variation in hemipteran assemblages using a canopy crane in a Bornean rain forest.

MATERIAL AND METHODS

Study site. The study was conducted in the Crane Plot (CP) (4 ha, 200 × 200 m) in Lambir Hills National Park, Sarawak, Malaysia (4°20’N, 113°50’E; 150–200 m asl; Yumoto & Nakashizuka, 2005). The park covers ca. 6,949 ha (Yumoto & Nakashizuka, 2005). The mean annual temperature is ca. 27°C (Kumagai et al., 2009), and the monthly temperature varies less than 2°C (Harrison, 2005). The mean annual rainfall in the park for the period 2000–2006 was approximately 2,600 mm (Kumagai et al., 2009). The drier months are from February through September and the wetter months are from October to January (Kumagai et al., 2009). During 2000–2006 periods, however, March and January were not always the driest and wettest periods, respectively (Kumagai et al., 2009). In the CP, for long-term monitoring, all trees over 10 cm in diameter at breast height (DBH, 1.3 m above the ground) were tagged and identified to species based on vegetative samples (Nakagawa et al., 2013). There were 2,365 trees belonging to 404 species in the CP (M. Nakagawa, unpubl. data). Dipterocarpaceae is the most abundant plant family, followed by Burseraceae and Euphorbiaceae (M. Nakagawa, unpubl. data). The CP contains an 85-m canopy crane with a jib length of 75 m (Sakai et al., 2002), which allows three-dimensional access to the tree crowns of about 200 trees of at least 70 species within 1.77 ha using a gondola attached to the jib on the crane. From the gondola, we determined the name of each tree using the number plates attached to the crowns that corresponded to the trees tagged and identified by ground-based monitoring. When the number plates were lost, we checked the location information of each tree crown visible in the operating room on the top of the crane and then checked the tags of the tree on the ground.

Sample collection. We sampled arthropods on the surface of tree crowns, where twigs and leaves are the main components, for 4–9 days during six time periods: September 2009 (9 days), February 2010 (7 days), April 2010 (4 days), August 2010 (5 days), September 2010 (4 days) and February 2011 (4 days). During each sampling period, we targeted 151–184 trees (Table 1) with a height range of 19.7–58.9 m. Weather conditions in the canopy, particularly rain and winds, often changed the numbers of trees that we accessed each sampling day; in adverse conditions, we were unable to access some of the target trees.

Arthropods were sampled from each target tree by sweeping 10 times from several clumps of leaves and twigs with a net (60 cm diameter, 100 cm depth) from the gondola of the crane. Each tree crown was spatially isolated from other crowns. The sampled arthropods were put into plastic bags, brought to the laboratory, kept in the freezer and then sorted to taxonomic order.

Sorting and identification. Of the arthropods collected over six sampling periods, Hemiptera adults and nymphs were the second most abundant group (ca. 23%), surpassed only by Araneae (K. Kishimoto-Yamada, unpubl. data). Tadashi Ishikawa sorted hemipteran samples to morphospecies. Nymphs were identified only to the superfamily or family level, because diagnostic characteristics are poorly developed in nymphs. Voucher specimens were deposited at the Forest Research Centre of Sarawak in Kuching, Malaysia, and in the Kyoto University Museum, Japan.

Feeding types. We determined the feeding type for each of the abundant species based on information on feeding guilds for other species in the family, according to Hodkinson & Casson (1991). For herbivores, species were classified as phloem, xylem or leaf juice feeders, following Novotny et al. (2010). Some groups of hemipterans, particularly those in the family Miridae, have more than one feeding guild. For example, some *Campylomma* spp. feed on small arthropods, such as mites, aphids and thrips, along with plant material (e.g., Hirose et al., 1993; Reding et al., 2001). *Termatophylum* spp. also prey on small arthropods such as thrips (Nakatani, 1997). The majority of *Zanchius* spp. are associated with plants, but have some predaceous behaviours (Yasunaga, 1999). Therefore, we regarded all species with some predaceous feeding as belonging to opportunistic predator guilds.

Tree phenology. We roughly assessed the phenological condition of target trees during each sampling event (Fig. 1). Based on characteristics observed at the sampling site, trees were placed into the following categories: 1) mature, immature leaves and other reproductive organs absent; 2) immature, at least a few immature leaves present and no evidence of reproductive organs; 3) bud, at least one bud visible; 4) flower, at least one flower visible; 5) seed, at least one seed visible. At the regional scale, the GF period was defined as the time when more than 6% of canopy trees (ca. 500) in the 8 ha plot within the park were flowering. In this study, GF occurred between April and November 2009 (S. Sakai, unpubl. data). During that time, the proportion of trees with buds, flowers or seeds was higher than in other periods (Fig. 1).

Data analyses. To estimate the completeness of sampling in each sampling period, we calculated species accumulation curves for adult hemipteran assemblages, based on individuals collected from all trees sampled at each sampling event, using EstimateS ver. 9.10 (Colwell, 2013).

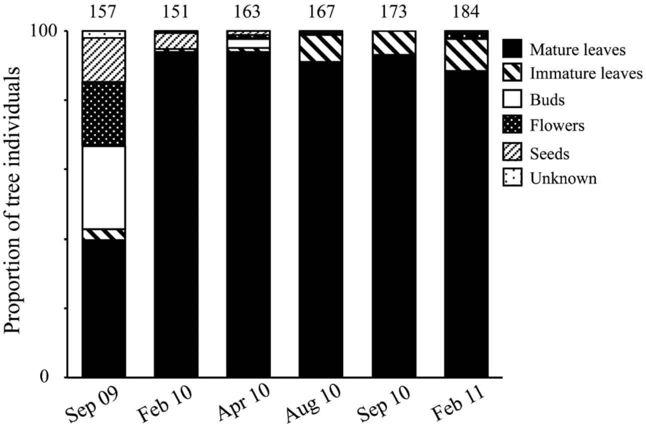

Fig. 1. Proportions of target canopy tree individuals with mature leaves, immature leaves, buds, flowers or seeds (see text for definitions). Numbers above bars represent the number of target trees during each sampling period.

We evaluated patterns of temporal fluctuation in the number of species and individuals of hemipteran adults, and the number of nymphs on each target tree during the six study periods. The total numbers of species and individuals on each target tree in each study period were log-transformed using $\log(x + 0.5)$ as per Yamamura (1999). The homogeneity of variance was unequal for all combinations (Bartlett tests, $p < 0.01$ for the individual numbers of adults and nymphs, $p=0.016$ for the number of adult species), so we performed a Kruskal–Wallis rank sum test with Nemenyi post hoc tests in the PMCMR package ver. 1.0 (Pohlert, 2015) of R statistical software ver. 3.1.2 (R Core Team, 2014).

In addition, to evaluate the similarity in the species composition of hemipteran adults among the study periods, we generated a two-dimensional ordination of the matrix using nonmetric multidimensional scaling (NMDS) in the vegan package ver. 2.2-1 of R (Oksanen, 2013). For this analysis, to equal sampling effort, we used adult data collected from 130 trees over the six study periods. We used the Sørensen similarity index based on presence/absence data for all species and the Bray–Curtis dissimilarity index based on abundance data for abundant species (≥ 10 individuals in 780 tree collections: 130 trees × 6 periods).

To evaluate the effects of GF and tree family on species-level abundance and occurrence, we constructed a zero-inflated Poisson model (see Martin et al., 2005), which is appropriate for modelling count data with many zero values, using data from the 33 abundant species (those with ≥ 10 individuals in 995 tree collections during the six sampling periods). This modelling method can analyse count data as a mixture of a Poisson component (model abundance) and a logistic compornent (model occurrence). In our analysis, we tested whether the GF event (September 2009) or non-GF periods (all others) determined the abundance (the number of insects observed) of species (i.e., the Poisson part) and

Table 1. List of tree species and the number of tree individuals that we assessed in each sampling period.

Family	Species	2009	2010				2011
		Sep	Feb	Apr	Aug	Sep	Feb
Cornaceae	*Mastixia* sp.	1	1	1	1	1	1
Ebenaceae	*Diospyros areolata*	1	1	1	1	1	1
	Diospyros dictyoneura	2	1	2	2	2	2
	Diospyros simaloerensis	0	1	0	0	1	1
Sapotaceae	*Madhuca crassipes*	2	2	3	3	3	3
	Madhuca sessilis	2	2	2	2	2	2
	Palaquium sp.	1	1	1	1	1	2
	Payena endertii	0	1	1	1	1	1
	Pouteria malaccensis	2	2	2	2	2	2
Fabaceae	*Dialium indum*	0	0	1	1	1	1
	Dialium platysepalum	0	0	0	0	0	1
	Koompassia malaccensis	3	4	4	4	4	5
	Sindora coriacea	1	1	1	1	1	1
Fagaceae	*Lithocarpus luteus*	1	1	1	1	1	1
Gentianaceae	*Fagraea caudata*	1	1	1	1	1	1
Rubiaceae	*Mussaendopsis beccariana*	1	1	1	1	1	1
Lamiaceae	*Teijsmanniodendron simplicifolium*	2	2	2	2	2	2
Lauraceae	*Endiandra* sp. aff. *srobiculata*	1	1	1	1	1	1
Annonaceae	*Mezzettia macrocarpa*	1	1	1	1	1	1
Myristicaceae	*Gymnacranthera bancana*	4	4	4	4	4	4
	Myristica gigantea	1	1	1	1	1	1
	Myristica smythiesii	0	0	0	0	0	1
Magnoliaceae	*Magnolia ashtonii*	2	1	2	2	2	2
Achariaceae	*Hydnocarpus castanea*	1	1	0	1	1	1
Calophyllaceae	*Calophyllum* sp. aff *soulattri*	1	1	1	1	1	1
Clusiaceae	*Garcinia parvifoli*a	1	1	1	1	1	1
Euphorbiaceae	*Blumeodendron calophyllum*	1	0	0	0	1	1
	Endospermum diadenum	2	2	3	3	2	3
	Ptychopyxis glochidiifolia	1	0	1	1	1	1
Ixonanthaceae	*Allantospermum borneense*	5	4	4	5	5	5
Ctenolophonaceae	*Ctenolophon parvifolius*	1	1	1	1	1	1
Dipterocarpaceae	*Dipterocarpus globosus*	5	5	5	5	5	6
	Dipterocarpus stellatus	1	1	1	1	1	2
	Dryobalanops aromatica	7	7	7	7	9	8
	Shorea acuta	9	9	9	9	9	9
	Shorea beccariana	17	19	18	18	18	21
	Shorea bullata	2	2	2	2	2	2
	Shorea crassa	6	6	6	6	6	6
	Shorea curtisii	2	1	2	2	2	2
	Shorea exelliptica	2	2	2	2	2	2
	Shorea fallax	3	3	3	3	3	3
	Shorea kunstleri	7	6	7	7	7	7
	Shorea laxa	2	2	2	2	2	2
	Shorea ochracea	1	1	1	1	1	1
	Shorea quadrinervis	1	1	1	1	1	1
	Shorea sp. cf. *ovata*	1	1	1	1	1	1
	Vatica micrantha	1	1	1	1	1	1
	Vatica oblongifolia	1	1	1	1	1	1

Family	Species	2009	2010				2011
		Sep	Feb	Apr	Aug	Sep	Feb
Malvaceae	*Durio lanceolatus*	1	1	1	1	1	1
	Durio sp.	1	1	1	1	1	1
	Pentace adenophora	0	1	1	1	1	1
	Pentace borneensis	2	2	2	2	2	2
	Scaphium macropodum	2	1	1	2	2	3
Myrtaceae	*Eugenia megalophylla*	0	1	1	0	1	1
	Eugenia ochneocarpa	1	1	1	1	1	1
	Eugenia sp.	2	2	2	2	2	2
Cannabaceae	*Gironniera hirta*	1	0	1	1	1	1
Moraceae	*Artocarpus anisophyllus*	4	3	4	4	5	4
	Artocarpus obtusus	1	1	1	1	1	1
	Parartocarpus venosus	0	1	1	1	1	1
Anacardiaceae	*Parishia sericea*	0	1	1	0	1	1
	Swintonia acuta	10	6	9	10	10	10
	Swintonia foxworthyi	5	6	6	7	6	7
	Swintonia sp.	3	3	3	3	4	5
Burseraceae	*Canarium apertum*	1	1	1	1	1	1
	Dacryodes incurvata	1	1	1	1	1	1
	Dacryodes sp.	1	0	1	1	1	1
	Santiria grandiflora	1	1	1	1	1	1
	Santiria griffithii	2	2	2	2	3	3
	Santiria laevigata	2	3	3	3	2	3
	Santiria mollis	5	4	5	5	5	4
	Santiria sp.	1	0	0	1	1	1
Total numbers of the studied tree individuals		**157**	**151**	**163**	**167**	**173**	**184**

if tree families determined the occurrence (presence or absence) (i.e., the logistic part) of each of the abundant species. Bayesian inference with Markov chain Monte Carlo (MCMC) simulations was used to estimate the parameters. We performed three chains of 10,000 steps each and sampled at 20-step intervals after a 5000-step burn-in. The priors for fixed-effect parameters were non-informative Gaussian distributions with mean 0 and variance 100. If the 95% credible interval (CI) of an explanatory variable did not include 0, we considered the variable significant. We used JAGS ver. 3.4.0 (Plummer, 2013) in the R ver. 3.0.2 (R Core Team, 2013) package R2jags ver. 0.03-11 (Su & Yajima, 2013) for calculations.

RESULTS

Hemipteran assemblage structures in the forest canopy. In total, we collected 1,172 hemipteran adults of 248 species and 431 nymphs. Cicadellidae was the most abundant adult in terms of both species and individual numbers, followed by Miridae (Table 2). Of adults, 42% were singletons (106 species). Although species accumulation curves for hemipteran adults did not reach an asymptote for any of the study periods, the total species number observed in September 2009 was higher than in the other periods (Fig. 2).

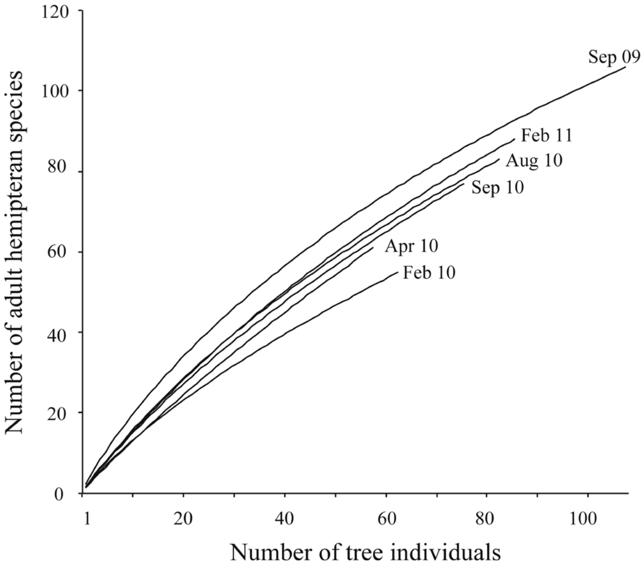

Fig. 2. Species accumulation curves (Sobs, Mao Tau) for adult hemipteran species during each sampling period. The curves are the result 50 randomisations.

Table 2. List of hemipteran species captured in the crowns of canopy trees. The number of each species collected in each sampling period is shown in parentheses.

	Total Numbers of Adult Species	Individual Numbers of Adults						Individual Numbers of Nymphs					
		2009	2010				2011	2009	2010				2011
		Sep	Feb	Apr	Aug	Sep	Feb	Sep	Feb	Apr	Aug	Sep	Feb
Sternorrhyncha													
Psylloidea	16	30 (9)	26 (3)	7 (5)	10 (6)	5 (4)	15 (4)	–	–	–	–	–	–
Auchenorrhyncha													
Cicadoidea													
Cidadidae	1	1 (1)	0	0	0	0	0	–	–	–	–	–	–
Cercopoidea													
Cercopidae	4	4 (2)	0	2 (2)	0	0	2 (2)	–	–	–	–	–	–
Machaerotidae	3	0	0	0	1 (1)	2 (2)	1 (1)	–	–	–	–	–	–
Membracoidea													
Cicadellidae	71	134 (31)	15 (9)	14 (12)	65 (27)	59 (26)	89 (33)	54	13	11	23	22	26
Membracidae	9	3 (3)	2 (2)	3 (2)	2 (2)	3 (3)	4 (3)	3	2	0	0	0	2
Fulgoroidea								36	18	36	69	34	47
Achilidae	11	7 (5)	7 (2)	6 (4)	11 (5)	4 (3)	6 (3)	–	–	–	–	–	–
Cixiidae	3	2 (1)	3 (1)	2 (2)	1 (1)	0	1 (1)	–	–	–	–	–	–
Delphacidae	1	4 (1)	0	0	0	0	3 (1)	–	–	–	–	–	–
Derbidae	13	4 (4)	7 (4)	1 (1)	12 (5)	7 (3)	20 (9)	–	–	–	–	–	–
Dictyopharidae	1	1	0	0	0	0	0	–	–	–	–	–	–
Flatidae	6	5 (3)	1 (1)	11 (4)	2 (2)	2 (2)	3 (2)	–	–	–	–	–	–
Issidae	8	20 (6)	9 (5)	3 (3)	11 (3)	17 (6)	6 (2)	–	–	–	–	–	–
Meenoplidae	1	2 (1)	4 (1)	1 (1)	3 (1)	2 (1)	8 (1)	–	–	–	–	–	–
Tropiduchidae	6	5 (3)	1 (1)	3 (3)	3 (1)	4 (2)	1 (1)	–	–	–	–	–	–
Heteroptera													
Dipsocoroidea													
Ceratocombidae	1	0	0	0	0	1	0	–	–	–	–	–	–
Schizopteridae	2	0	0	0	0	1 (1)	2 (2)	–	–	–	–	–	–
Reduvoidea													
Reduviidae	4	1 (1)	1 (1)	2 (1)	1 (1)	0	0	–	–	–	–	–	–
Miroidea													
Miridae	43	152 (18)	6 (5)	7 (5)	31 (12)	17 (10)	22 (13)	7	0	1	2	3	7
Tingidae	12	12 (5)	15 (6)	4 (2)	33 (6)	10 (5)	5 (4)	–	–	–	–	–	–
Cimicoidea													
Anthocoridae	5	10 (3)	0	0	2 (2)	0	0	3	0	0	0	0	0

Table 2...Continued

	Total Numbers of Adult Species	Individual Numbers of Adults						Individual Numbers of Nymphs					
		2009	2010				2011	2009	2010				2011
		Sep	Feb	Apr	Aug	Sep	Feb	Sep	Feb	Apr	Aug	Sep	Feb
Penatomoidea													
Cydnidae	1	1	0	0	0	0	0	–	–	–	–	–	–
Pentatomidae	2	2 (1)	2 (2)	5 (2)	0	0	0	2	0	0	0	0	3
Plataspidae	12	8 (6)	19 (8)	12 (7)	9 (6)	11 (5)	11 (4)	–	–	–	–	–	–
Tessaratomidae	1	0	0	2 (1)	0	0	2 (1)	–	–	–	–	–	–
Pyrrhocoroidea													
Largidae	1	0	0	1	0	0	0	–	–	–	–	–	–
Lygaeoidea													
Geocoridae	1	0	1 (1)	0	0	0	0	–	–	–	–	–	–
Lygaeidae	4	0	5 (1)	0	2 (1)	3 (3)	1 (1)	–	–	–	–	–	–
Rhyparochromidae	2	0	0	1 (1)	1 (1)	0	0	–	–	–	–	–	–
Unknown	3	0	1 (1)	2 (2)	0	0	0	0	4	1	1	1	0

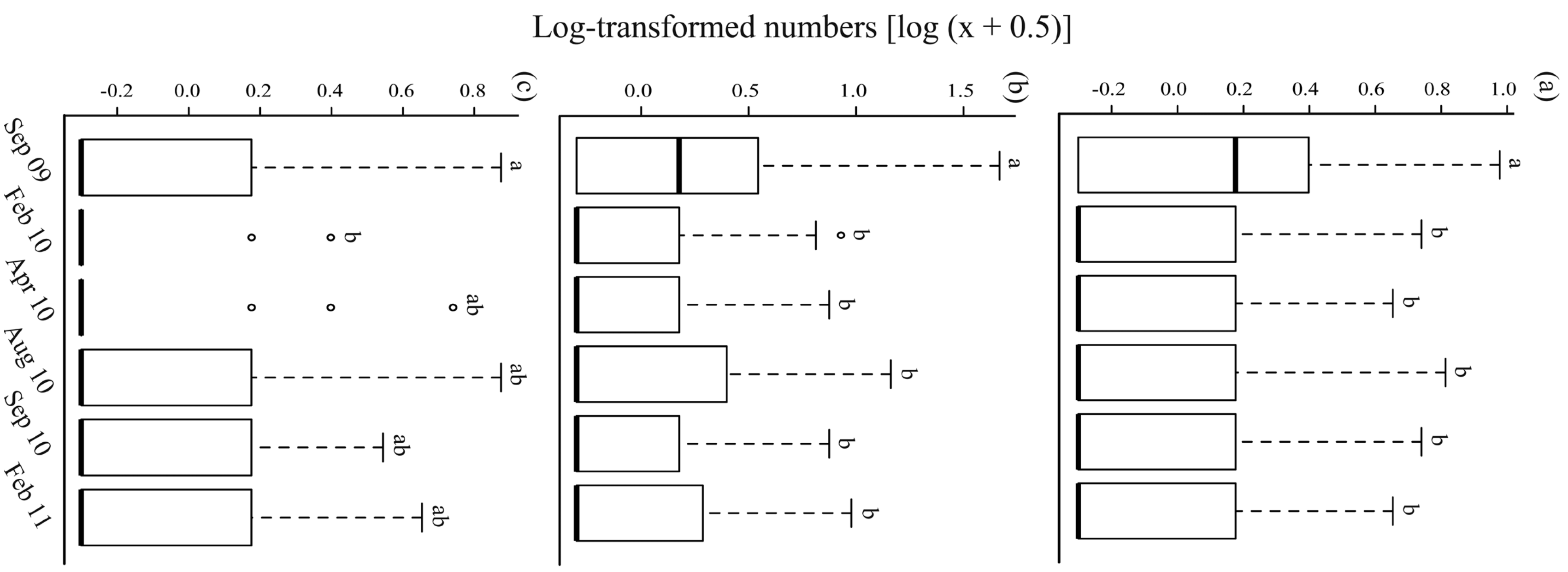

Fig. 3. Log-transformed numbers of (a) adult species, (b) adult individuals and (c) nymphs during each sampling period. Different letters indicate significant differences in abundance (Kruskal–Wallis with post hoc tests, $p < 0.01$). Box plots indicate the range of the data within the ends of the whiskers; the middle two quartiles are within the box; and the median value is indicated by the bold line. The end of the whisker indicates Q3 + 1.5×(Q3 – Q1) and the outliner is above it.

Table 3. Summary of zero-inflated Poisson mixture models for the effects of GF and tree family on the abundance of 33 abundant hemipteran species.

Species	Feeding Type	GF coefs.	Tree Family (Ref. Achariaceae)																							
			Cor	Ebe	Sap	Fab	Fag	Gen	Rub	Lam	Lau	Ann	Myi	Mag	Cal	Clu	Eup	Ixo	Cte	Dip	Mal	Myr	Can	Mor	Ana	Bur
Psylloidea sp.4	Phloem			■																						
Psylloidea sp.5	Phloem	+	■			■													■	▨						
Psylloidea sp.10	Phloem							■												■					■	
Idiocerinae sp.1	Xylem	+												■						▨	■				■	■
Macropsinae sp.1	Xylem	+											■							■						
Macropsinae sp.3	Xylem	+		▨													▨			▨					▨	
Typhlocybinae sp.1	Leaf					■										■				■						■
Typhlocybinae sp.2	Leaf	+				■											■			■					■	
Typhlocybinae sp.3	Leaf																			■						■
Typhlocybinae sp.4	Leaf																			■	■					
Typhlocybinae sp.6	Leaf																			▨	▨				▨	▨
Typhlocybinae sp.7	Leaf				■	■						■								■						
Typhlocybinae sp.11	Leaf																				■					■
Typhlocybinae sp.13	Leaf					■											■			■						■
Typhlocybinae sp.21	Leaf	−																▨		▨						▨
Achilidae sp.1	Phloem																			■					■	
Achilidae sp.2	Phloem		■																							
Derbidae sp.8	Phloem	−			■											■				▨		■			■	
Flatidae sp.4	Phloem			▨	▨															▨					▨	▨
Issidae sp.2	Phloem				▨								▨					▨		▨					▨	▨
Issidae sp.6	Phloem	+			▨															■				▨	▨	
Meenoplidae sp.1	Phloem				▨													▨		▨	▨			▨	▨	▨
Campylomma sp.1	OP	+	■	■		■														■	■				▨	
Termatophylum sp.1	OP	+			■	■														■						
Termatophylum sp.2	OP	+				■														■						■

Species	Feeding Type	GF coefs.	Tree Family (Ref. Achariaceae)																							
			Cor	Ebe	Sap	Fab	Fag	Gen	Rub	Lam	Lau	Ann	Myi	Mag	Cal	Clu	Eup	Ixo	Cte	Dip	Mal	Myr	Can	Mor	Ana	Bur
Zanchius sp.1	OP				■				■											■			■			■
Tingidae sp.2	Leaf		▒		▒											▒				▒						▒
Tingidae sp.3	Leaf									■										■						■
Tingidae sp.7	Leaf												■													
Tingidae sp.8	Leaf									■										■						■
Plataspidae sp.1	Leaf										■		■													
Plataspidae sp.2	Leaf												■													
Plataspidae sp.3	Leaf	–											■													

GF coefs.: + and − indicate significant positive and negative coefficients, respectively. Black boxes indicate significant positive coefficients. Grey boxes denote non-significant coefficients, although at least one individual was caught. Significance means that the 95% credible interval (CI) of an explanatory variable did not include 0. Tree Family: Cor, Cornaceae; Ebe, Ebenaceae; Sap, Sapotaceae; Fab, Fabaceae; Fag, Fagaceae; Gen, Gentianaceae; Rub, Rubiaceae; Lam, Lamiaceae; Lau, Lauraceae; Ann, Annonaceae; Myi, Myristicaceae; Mag, Magnoliaceae; Cal, Calophyllaceae; Clu, Clusiaceae; Eup, Euphorbiaceae; Ixo, Ixonanthaceae; Cte, Ctenolophonaceae; Dip, Dipterocarpaceae; Mal, Malvaceae; Myr, Myrtacea; Ana, Anacardiaceae; Bur, Burseraceae. Achariaceae was chosen as the reference category. OP: Opportunistic Predators.

Temporal patterns in assemblages. Significantly more species and individuals of adults were collected in September 2009, during the GF event, than in any other study period (Fig. 3a, b; Kruskal–Wallis with post hoc tests, $p < 0.01$). For the nymphs, the individual numbers caught in September 2009 were significantly higher than those in February 2010 (Fig. 3c; Kruskal–Wallis with post hoc tests, $p < 0.01$).

In the NMDS ordination of adult assemblages based on presence/absence data, each study period group was located separately (Fig. 4a), suggesting that species compositions differed among study periods. In the NMDS plot of adult assemblages based on abundance data, groups collected in the latter part of the study (August 2010, September 2010, February 2011) clustered closely together, while groups collected in the earlier part of the study (September 2009, February 2010, April 2010) were distinct (Fig. 4b), suggesting that species compositions of abundant species varied in the earlier study periods but became more similar during the later sampling periods.

Effects of GF and tree families on abundant species. Our models showed significantly higher abundances of insects during the GF period than during the non-GF periods for nine of the 33 abundant species (Table 3). Of the nine species, Psylloidea sp. 5, *Termatophylum* sp. 1, and *Termatophylum* sp. 2 were caught only in the GF event. For the other six species, most individuals were caught on canopy trees with immature and/or mature leaves during the non-GF periods. Six of these nine species were herbivores, including phloem, xylem and leaf suckers, and three were opportunistic predators (Table 3).

Five species (Psylloidea sp. 4, Achilidae sp. 2, Tingidae sp. 7, Plataspidae sp. 2, and Plataspidae sp. 3) were collected only from a single tree family and included phloem and leaf suckers (Table 3).Other species showed non-significant occurrences on one particular tree family, and these species often occurred on more than two tree families (Table 3). This tendency was found among phloem, xylem and leaf suckers (Table 3).

DISCUSSION

This study investigated 184 canopy trees from 25 different families, using a canopy crane in a Bornean rain forest. Few studies have targeted such numerous and diverse canopy trees to sample the canopy arthropods. In addition, we repeatedly sampled arthropods in the canopy and our study encompassed a significant flowering event of many canopy tree species. However, despite our large sampling effort involving numerous target trees and the flowering period, the proportion of singletons was high. This tendency is often observed for insect groups in tropical forests (e.g., Allison et al., 1997; Basset, 1997; Novotny & Basset, 2000). The high proportion of the singletons may be attributable to ecological traits such as diffusion and association with specific plants (Novotny & Basset, 2000) or may be due to insufficient sampling (Coddington et al., 2009). Our study primarily surveyed the hemipteran assemblage foraging on

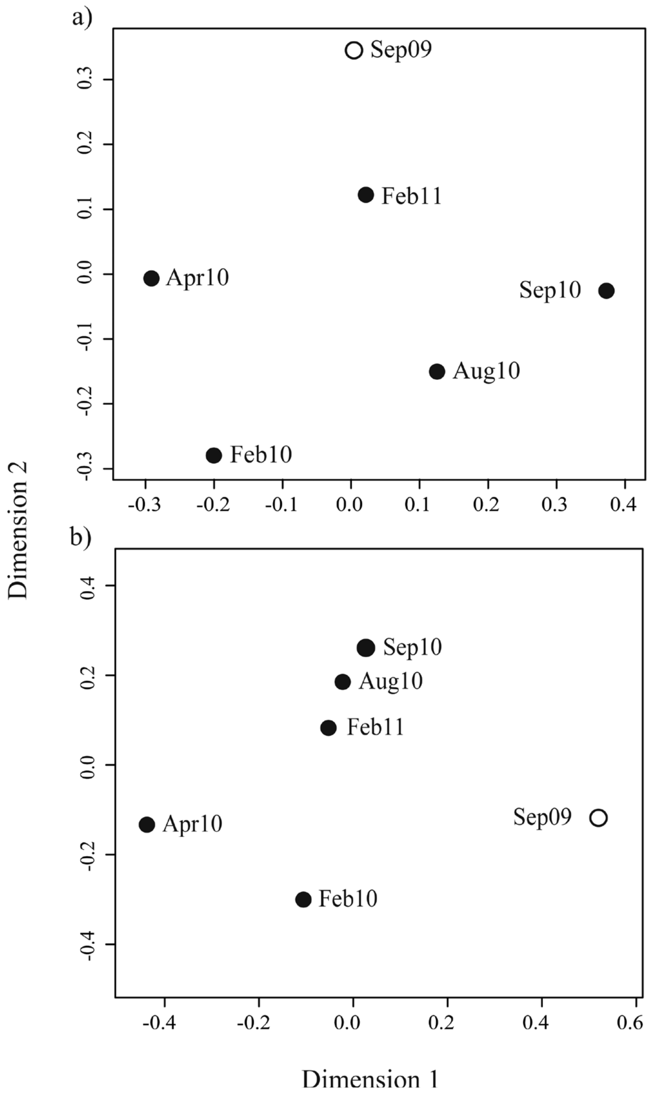

Fig. 4. NMDS ordination plots for (a) all species based on the Sørensen similarity index and (b) abundant species based on the Bray–Curtis dissimilarity index. White circle indicates the GF period and black circle indicates the non-GF period.

the surface of the canopy tree crowns. Further investigations of arthropods foraging in the interior of crowns may be required to enhance our knowledge regarding the structure of hemipteran assemblages in tropical forest canopies.

Our canopy crane approach revealed patterns of temporal fluctuation in adult hemipteran assemblages. In particular, GF events caused dynamic changes in adult species diversity and species composition. Our study showed relatively high proportions of flowers, buds and seeds during the GF event compared to non-GF periods. Phytophagous hemipteran species feed on a wide variety of plant parts and many prefer flowers, buds and seeds (Schuh & Slater, 1995). Therefore, these resources seem to be valuable for canopy-foraging phytophagous hemipteran adults at our study site.

GF events may also increase the diversity of opportunistic predatory hemipterans. *Campylomma* and *Termatophylum*, which prey on small arthropods such as thrips (Hirose et al., 1993; Nakatani, 1997; Reding et al., 2001), increased markedly in abundance during the GF event. Moreover, two *Termatophylum* species did not appear during non-GF periods. We observed that the number of thrips during the GF event was roughly 350 times higher than during non-GF events (K. Kishimoto-Yamada et al., unpubl. data). Such a dramatic increase of thrips and possibly other arthropods may attract these hemipteran species, resulting in the high density observed in this study. Moreover, it is possible that the high density is caused by the increase in plant materials, such as flowers, buds, and seeds available during GF events since they have more than one feeding guild. Detailed investigations are required to determine what resources that directly influence the abundance of these opportunistic predators.

As GF events occur at supra-annual and irregular intervals (Appanah, 1985; Ashton et al., 1988; Sakai et al., 1999a; Sakai, 2002), it is not clear how hemipteran adults that rely on plant or animal materials that increase during GF events survive during non-GF periods. Three possible strategies have been demonstrated empirically: (1) immigration; (2) short-term reproduction; and (3) resource switching between GF and non-GF periods. For example, *Apis dorsata*, which are pollinators of various canopy trees during GF events (Momose et al., 1998) immigrate to forests where GFs occur (Itioka et al., 2001). Pollinator thrips tend to reproduce rapidly during GF periods, while they maintain their populations at low levels on the forest floor during non-GF periods (Appanah & Chan, 1981; Ashton et al., 1988). Canopy-foraging chrysomelid beetles, which are presumed to be pollinators of canopy trees during GF periods (Sakai et al., 1999b), tend to switch their food resources from young leaves to flowers (Kishimoto-Yamada & Itioka, 2008). Any of these strategies allow the survival of canopy foraging hemipteran populations through GF and non-GF periods. Alternatively, hemipterans may concentrate on the inner or lower parts of tree crowns during non-GF periods, and move into the upper canopy layer during GF periods to seek temporary high-quality resources, such as seeds, buds, and flowers. Currently, insufficient information is available on the ecological traits of canopy-foraging hemipterans to determine which hypothesis is the most likely. Further studies should focus on the life-history strategies of canopy-foraging hemipterans.

The result of the NMDS ordination plots for the abundant species showed that species compositions were similar among three study periods: August 2010, September 2010 and February 2011. This high similarity seems to be due to the short interval between August and September. In addition, the high occurrence of young leaves may determine species composition, which has been shown to be an important factor in determining herbivore communities in tropical forest canopies (Basset, 1991; Kishimoto-Yamada & Itioka, 2008).

For the abundant hemipteran species, herbivores that specialise on certain tree families appear to be rare in the Bornean rain forest canopy. A study in Papua New Guinea (PNG) rainforests clearly demonstrated that specialisation on certain plant families was rare for phloem- and xylem-sucking insects (Novotny et al., 2010). This study also confirmed that most phloem and xylem suckers occurred on more than one plant family. For leaf-sucking species, however, our result showed that only 3 of the 16 leaf-sucking species appeared on a single tree family and the tendency seems to differ from their result: all of the leaf-sucking species in the PNG rain forest specialised on a single family (Novotny et al., 2010). Our study did not exclude possible tourist species, which accidentally occur on trees without having an ecological relationship with the species. Consequently, further investigations including rearing and feeding trials on host plants of canopy foraging hemipteran adults are needed to clarify the degree of specialisation.

This study highlights the usefulness of canopy cranes for characterising assemblages of canopy arthropods, as has been shown previously (Ødegaard, 2000, 2004, 2006; Basset, 2001b; Kitching et al., 2007; Wardhaugh et al., 2012; Wardhaugh, 2014; Katayama et al., 2015). Recently, research productivity using canopy cranes has decreased (Novotny & Miller, 2014). Studies on arthropod communities in tropical forest canopies are essential to better understand terrestrial arthropod diversity. As Novotny & Miller (2014) argued in their review, coordinated studies among permanent plots equipped with canopy cranes will enhance our knowledge of canopy arthropod diversity.

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