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Species Diversity and Vertical Distributions of Weevils (Coleoptera, Curculionidae) Collected by Collision Traps with Floral-fragrance Attractants in a Bornean Rainforest

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Abstract Tropical rainforests have high levels of insect diversity in a vertical forest structure. We collected weevils (Curculionidae) in a lowland dipterocarp forest in the Lambir Hills National Park, Sarawak, Malaysia using collision traps with floral-fragrance attractants, which we set at heights of 25–45 m and 2 m above the ground. A total of 5,121 weevils were collected and identified to 49 morphospecies in seven subfamilies. Not only the weevil abundance and species richness, but also the dominance of abundant species, was higher in the tropical rainforest than in temperate forests in Wakayama, Japan. In the tropical rainforest, more weevils were collected by high traps than by low traps, and the frequency of weevils collected by high traps varied among species. These results suggest a higher diversity of flower-visiting weevil species in tropical rainforests than in temperate forests and a difference in vertical distributions among weevil species in tropical rainforests.

Introduction

Tropical rainforests in Southeast Asia are characterized by warm, wet and aseasonal climates (KUME *et al.*, 2011; KISHIMOTO-YAMADA & ITIOKA, 2015). These rainforests have a complex vertical forest structure with multiple canopy layers and emergent trees (KUMAGAI *et al.*, 2001), which allows them to support high levels of insect diversity (KATO *et al.*, 1995). In addition, the occurrence of general flowering, the phenomenon where flowering is synchronized across diverse plant taxa at irregular intervals spanning several years (SAKAI *et al.*, 1999 b), can affect insects that depend on floral resources in the rainforests (KISHIMOTO-YAMADA & ITIOKA, 2008). The rainforests are also characterized by the prevalence of beetle pollination (MOMOSE *et al.*, 1998). Among beetles, leaf beetles (Chrysomelidae) are important pollinators (SAKAI *et al.*, 1999 a) that exhibit a variety of population fluctuations in response to supra-annual drought and general flowering (KISHIMOTO-YAMADA *et al.*, 2009). However, other beetle taxa, such as weevils (Curculionidae), have not been investigated intensively, even though they also visit flowers and act as pollinators (CORLETT, 2004).

Flower-visiting weevils are attracted by volatile floral compounds. Field tests of fragrance chemicals show that traps baited with benzyl acetate, methyl benzoate, or linalool catch weevils (MAETÔ *et al.*, 1995). Since such trapping has been conducted in various forests in Asia, including temperate forests in Japan (MIZOTA & IMASAKA, 1997), the abundance and diversity of flower-visiting weevils can be compared between tropical and temperate forests in Asia.

In tropical rainforests, environmental conditions and resource availability are different between the canopy and understory (KUMAGAI *et al.*, 2001). Flower-visiting beetles were more frequently collected by traps set in the canopy than by traps in the understory, suggesting the existence of suitable environmental conditions and abundant floral resources in the canopy (FUKUYAMA *et al.*, 1994). On the other hand, some understory plants provide their pollinators with specific floral resources, and niche differentiation in flower-visitors can occur between the canopy and understory (KATO, 1996). It is therefore considered likely that the vertical distribution of flower-visiting weevil species also varies in relation to the vertical forest structure.

Here, we report on the weevil fauna collected by collision traps with floral-fragrance attractants in a Bornean rainforest. We compared the faunal assemblage in the tropical rainforest with those collected by the same traps in Japanese temperate forests. In addition, we conducted trapping in the canopy and understory of the rainforest and compared the vertical distributions of the collected weevil species.

Material and Methods

Traps for collecting flower-visiting insects were set at the Canopy Biology Plot (4°20'N, 113°50'E, 150–250 m above sea level), in a lowland dipterocarp forest in the Lambir Hills National Park, Sarawak, Malaysia (KATO *et al.*, 1995; MOMOSE *et al.*, 1998; SAKAI *et al.*, 1999 b). The traps (Sankei Chemical Co., Ltd.; 25 cm in diameter, 42 cm in height) consisted of white- or yellow-colored plastic components, a roof on the top, two intersecting collision plates in the middle, and a bucket at the bottom. A cotton ball infused with 15 ml of mixed solution of benzyl acetate and linalool (1 : 1) was placed at the center of each trap. The bucket was filled with 50% propylene glycol and surfactant.

Three white traps and three yellow traps were set at each height of 25–45 m and 2 m above the ground (12 traps in total). The traps were suspended from wire cables of canopy walkways (25–45 m), or from strings tied between trees (2 m). These traps were set in three durations: 20–28 December 2007 (8 days; period 1), 5–15 March 2008 (10 days; period 2), and 12–21 August 2008 (9 days; period 3), with traps set-up and retrieved at around noon on the first and last day of these periods, respectively. All of the insects trapped during the periods were collected. General flowering did not occur in these periods (KOBAYASHI *et al.*, 2013). Temperatures were lower during period 1 than during periods 2 and 3 (KUME *et al.*, 2011; KOBAYASHI *et al.*, 2013).

Collected insects were pinned, dried, labeled, and deposited at the Forest Research Centre of Sarawak, Kuching and the Laboratory of Entomology, Tokyo University of Agriculture, Atsugi. The specimens were sorted into families, and weevils (Curculionidae) were selected for further analysis. Selected specimens were identified to morphospecies (referred to as species hereafter) and classified into subfamilies.

To compare the abundance and species diversity of weevils collected in the Bornean rainforest with those collected using the same traps baited with benzyl acetate in temperate forests, we obtained weevil fauna in six forests in Wakayama Prefecture, Japan (MIZOTA & IMASAKA, 1997). Because MIZOTA and IMASAKA (1997) used white traps at a height of 3 m above the ground, we restricted the comparison to the weevil fauna collected by white traps at a height of 2 m in the Bornean rainforest. The abundance, species richness, and trapping effort (the number of traps and trapping days) were

compared between this study and that of MIZOTA and IMASAKA (1997). Species-abundance curves, relationships between the logarithmically-scaled relative frequency on the Y-axis and the abundance rank on the X-axis, were produced for both fauna.

Finally, preference in height and color of traps were examined using generalized linear mixed models. Response variables of the model for height or color preference were the number of weevils collected by high and low or white and yellow traps, respectively. The response variables followed a binomial distribution with two parameters, the probability of catch by high or white traps and the sample size. We examined whether each of the height and color preferences differed among the periods, between the trap properties, and among weevil species. A predictor for the height preference model consisted of an intercept (the probability of catch by high and white traps in period 1), fixed effects of periods 2 and 3, a fixed effect of yellow color, and a random effect of weevil species. A predictor for the color preference model consisted of the intercept, fixed effects of periods 2 and 3, a fixed effect of weevil species. The random effect followed a Gaussian distribution with mean = 0 and standard deviation (SD). The models were fitted to the data using glmmML (family = binomial (link = "logistic")) in R 3.0.2 (R Core Team, 2013). We tested whether the intercept, coefficients of the fixed effects, and the SD of the random effect differed from 0 using the Wald *t* test. When the SD of the random effect was significantly positive, the SD of each species was estimated from posterior modes in the output of glmmML.

Results

A total of 5,121 weevils were collected and identified to 49 species in seven subfamilies in Curculionidae (Table 1). Of these, the subfamily Curculioninae was dominant with 5,094 individuals and 37 species (Table 1). In the Curculioninae, the genus *Endaenidius* was dominant with 4,834 individuals and 20 species (Table 1). The highest number of weevils was collected in period 3 (2,297), followed by period 1 (1,719), and then period 2 (1,105). Markedly more weevils were caught by the high traps (4,638) than by low traps (483), and more weevils were collected by white traps (2,825) than by yellow traps (2,296).

Weevil fauna collected from the white traps at the low height were compared between the tropical and temperate forests. In the tropical rainforest, the fauna collected over 81 trap day (three traps for 27 days in the three periods) comprised 272 individuals of 20 species. In each of the six temperate forests, the fauna collected over 125 trap days (one trap for 125 days) comprised 6–39 individuals of 4–10 species. Compared to the temperate fauna, the species-abundance curve obtained from the tropical fauna indicated a steeper slope for abundant species and a longer tail for rare species (Fig.1).

Weevils exhibited greater preference for high traps over low traps and for white traps over yellow traps, which was indicated by the estimated intercepts of the models being significantly positive $(P \le 0.003; \text{ Table 2})$. The probability of catch by high traps was higher in periods 2 and 3 than in period 1, because the estimated coefficients of the fixed effects were significantly positive $(P < 0.001; \text{ Ta$ $ble 2})$. The probability of catch by white traps was higher in period 1 than in periods 2 and 3, because the estimated coefficients of the fixed effects were significantly negative $(P \le 0.002; \text{ Table 2})$. Trap color did not affect the probability of catch by high traps, and trap height did not affect the probability of catch by white traps $(P \ge 0.867; \text{ Table 2})$. Preference in height differed among species, which was indicated by the estimated SD of the species random effect on the probability of catch by high traps was significantly positive (P < 0.001; Table 2). Among species for which five or more individuals were collected, the SD was > 2 in *Endaenidius kemae*, *E*. sp. 3, *E*. sp. 4, and *E*. sp. 5, while the SD was < -2 in *Endaenidius maetoi*, *E*. sp. 7, *Hexeria* sp., *Mecysmoderes* sp. 1, and Cyphicerini genus inTable 1. Number of weevils (Curculionidae) belonging to 49 morphospecies in seven subfamilies. Weevils were collected in three periods using white (W) and yellow (Y) traps at heights of 25–45 m (H) and 2 m (L) above the ground. Estimated standard deviation of a species random effect on probability of catch by high traps is listed for each species (see Table 2).

Subfamily	Period and trap											Species		
Morphospecies		2007 De				: 2008 N				: 2008 Au				effect
	HW	HY	LW	LY	HW	HY	LW	LY	HW	HY	LW	LY	Total	on height
Curculioninae														
Acalyptini gen. et sp. indet. 1	2	0	0	0	0	0	0	0	0	1	0	0	3	1.03
Acalyptini gen. et sp. indet. 2	0	0	0	0	0	1	0	0	0	0	0	0	1	0.32
Acalyptini gen. et sp. indet. 3	0	0	0	0	0	0	0	0	0	1	0	0	1	0.33
Acalyptini gen. et sp. indet. 4	0	0	0	0	0	0	0	0	1	0	0	0	1	0.34
Endaeus sp.1	1	4	2	6	19	16	5	15	13	6	4	2	93	-1.79
Endaeus sp.2	0	1	1	4	1	0	0	0	7	4	1	0	19	-1.30
Endaeus sp.3	1	2	1	0	1	1	0	1	0	0	0	0	7	-0.8
Endaeus sp.4 nr.testaceus	0	2	0	0	0	0	0	0	0	0	0	0	2	0.9
Endaeus sp.5	1	0	0	0	0	0	0	0	1	0	0	0	2	0.7
Endaens sp.6	0	0	0	0	0	1	0	0	0	0	0	0	1	0.3
Endaeus sp.7	0	1	0	0	0	0	0	0	0	0	0	0	I	0.6
Endaenidius kemae	18	17	0	0	19	20	1	0	14	14	0	0	103	2.2
Endaenidius maetoi	1	2	5	1	0	0	0	0	0	0	0	1	10	-2.2
Endaenidius sp.1	588	338	89	57	340	273	11	9	438	486	33	18	2,680	0.4
Endaenidius sp.2	44	41	26	19	72	58	14	26	173	144	51	26	694	-1.0
Endaenidius sp.3	153	81	3	1	21	0	0	0	256	257	3	3	778	2.2
Endaenidius sp.4	22	20	0	0	5	8	0	0	64	55	0	1	175	2.6
Endaenidius sp.5	76	66	1	0	70	53	0	I	20	19	0	2	308	2.3
Endaenidius sp.6	1	0	0	0	8	1	0	I	11	16	1	0	39	0.4
Endaenidius sp.7	1	0	1	0	2	0	0	3	0	0	0	0	7	-2.3
Endaenidius sp.8	0	1	0	0	1	0	1	0	0	0	0	0	3	-1.1
Endaenidius sp.9	0	0	0	0	0	2	0	0	0	0	0	0	2	0.5
Endaenidius sp.10	0	0	0	0	0	0	0	0	0	0	0	2	2	-3.3
Endaenidius sp.11	0	0	0	0	0	0	0	0	0	2	0	0	2	0.5
Endaenidius sp.12	0	1	0	0	0	1	0	0	0	0	0	0	2	0.7
Endaenidius sp.13	0	0	0	0	0	1	0	0	0	0	0	0	1	0.3
Endaenidius sp.14	0	0	0	0	0	0	0	0	0	0	1	0	1	-2.6
Endaenidius sp.15	0	0	0	0	0	0	0	0	1	0	0	0	1	0.3
Endaenidius sp.16	0	0	0	0	1	1	0	0	0	0	0	0	2	0.5
Endaenidius sp.17	0	1	0	0	0	0	0	0	0	0	0	0	1	0.6
Endaenidius spp. indet.	2	1	0	0	2	4	0	0	8	5	1	0	23	0.6
Hexeria sp.	0	0	1	2	0	0	1	0	0	0	2	0	6	-4.0
Heterochyromera sp.1	0	0	0	0	1	0	0	0	0	0	0	0	1	0.3
Heterochyromera sp.2	0	0	0	0	0	0	0	0	1	0	0	0	1	0.3
Heterochyromera sp.3	0	0	0	0	0	0	0	0	1	0	0	0	1	0.3
Ochyromerini gen. et sp. indet. 1	1	1	0	0	2	1	0	0	58	50	2	4	119	0.4
Ochyromerini gen. et sp. indet. 2	0	0	0	0	1	0	0	0	0	0	0	0	1	0.3
Cryptorhynchinae														
Cryptorhynchini gen. et sp. indet.	0	0	0	1	0	0	0	0	0	0	0	0	1	-2.0
Molytinae														
Alcidodes sp.1	0	0	0	0	0	0	0	0	0	0	0	1	1	-2.6
Baridinae														
Baridinae gen. et sp. indet. 1	0	1	0	0	1	0	0	0	0	0	0	0	2	0.7
Baridinae gen. et sp. indet. 2	0	1	0	0	0	0	0	0	0	0	0	0	1	0.6
Baridinae gen. et sp. indet. 3	0	0	0	0	2	0	0	0	0	0	0	0	2	0.5
Baridinae gen. et sp. indet. 4	0	0	0	0	0	0	0	0	1	0	0	0	1	0.3
Conoderinae														
Coryssomerini gen. et sp. indet. 1	0	0	0	0	0	0	0	0	0	0	1	0	1	-2.6
Coryssomerini gen. et sp. indet. 2	0	0	0	0	0	0	0	0	1	0	0	0	I	0.3
Ceutorhynchinae	-				-	-	-		_	-			-	
Mecysmoderes sp.1	0	0	3	0	0	0	1	0	0	0	3	0	7	-4.2
Entiminae	5	-	-	-	2	5		-	5	-		-		
Cyphicerini gen. et sp. indet. 1	0	0	0	1	0	0	0	2	0	1	1	1	6	-3.3
Cyphicerini gen. et sp. indet. 2	0	0	0	0	ĩ	0	0	0	0	0	0	0	1	0.3
Cyphicerini gen. et sp. indet. 3	0	0	Ő	õ	î	0	0	0	1	0	ĩ	ő	3	-1.3
Total	912	582	133	92	571	442	34	58	1,070	1,061	105	61	5,121	0.0

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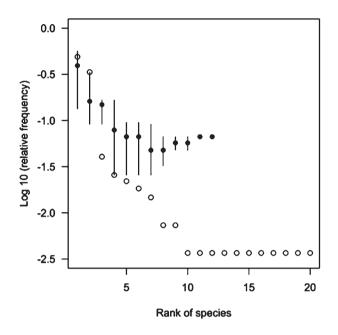


Fig. 1. Species-abundance curves of weevil fauna in a tropical rainforest (this study; open circles) and in six temperate forests (MIZOTA & IMASAKA, 1997; medians: closed circles, range: bars).

det. 1 (Table 1). Thus, the former set of species preferred high traps, while the latter set of species preferred low traps.

Discussion

In this study, the weevil fauna collected by collision traps baited with floral-fragrance attractants in a Bornean rainforest was dominated by the genus *Endaenidius* in the curculionine subtribe Ochyromerina of the tribe Tychiini. Weevils of this genus and *Endaeus* in Ochyromerina are both pollinators of annonaceous plants in tropical rainforests (MOMOSE *et al.*, 1998; GOTTSBERGER *et al.*, 2011). These plants are protogynous and often have white or yellow corollas and chamber- or cup-shaped flowers (MOMOSE *et al.*, 1998). The scent produced by the female stage attracts the weevils, which are retained in the floral chambers until they are released in the male stage. The weevils feed on various floral parts, use flowers as mating sites, and deposit their eggs on the floral tissue (GOTTSBERGER *et al.*, 2011). In addition to having white and yellow flowers, these floral characteristics suggest that white or yellow traps with floral fragrance strongly attract ochyromerine weevils.

Despite the lower trapping effort in this study, compared to MIZOTA and IMASAKA (1997), the number of individuals and species of trapped weevils were both higher in the tropical rainforest of Sarawak, Malaysia than in the temperate forests of Wakayama, Japan. Compared to the temperate forests, the higher abundance and species richness in the tropical rainforest may be partly due to different pollination systems in these two forests. Animal pollination is more widespread in tropical plant communities than in temperate plant communities (OLLERTON *et al.*, 2011). In tropical rainforests in Southeast Asia, animal pollination is dominated by social bees, with beetles probably the next most important group, followed by other bees and flies (MOMOSE *et al.*, 1998; CORLETT, 2004). Thus, the

Table 2. Results of two generalized linear mixed models for preference in height (top) and color (bottom). Coeffi-
cients of fixed effects of period and trap property and standard deviation of a random effect of species on
probability of catch by high traps (top) and white traps (bottom) were estimated.

Effect	Estimate	Standard error	P-value	
Probability of catch by high traps				
Intercept: period 1, white	1.492	0.501	0.003	
Period 2	1.024	0.148	< 0.001	
Period 3	0.964	0.124	< 0.001	
Yellow	0.017	0.105	0.867	
SD of species random effect	2.408	0.466	< 0.001	
Probability of catch by white traps				
Intercept: period 1, high	0.439	0.051	< 0.001	
Period 2	-0.248	0.078	0.002	
Period 3	-0.392	0.065	< 0.001	
Low	-0.001	0.097	0.995	
SD of species random effect	0.000	0.035	0.500	

prevalence of beetle pollination in the Bornean rainforest may result in rich floral resources to flower-visiting weevils, which may lead to their high abundance and diversity. The species-abundance curve obtained from the Bornean rainforest fauna indicates that only a few abundant species contribute to the high abundance, and that many rare species contribute to the high diversity. Given that species abundance distributions are affected by a variety of factors (McGILL *et al.*, 2007), determining the factors responsible for the observed patterns in the tropical fauna is difficult.

As expected from FUKUYAMA *et al.* (1994), flower-visiting weevils preferred high traps that were set at heights of 25–45 m above the ground. In the Bornean rainforest, the relative abundance of light-trapped weevils was highest in the canopy layer (25, 35 m), compared with the emergent layer (45 m) and understory layers (1, 5, 17 m) (KATO *et al.*, 1995). Weevils are thus abundant in the rainforest canopies, where floral resources are abundant. Height preference differed among flower-visiting weevil species. Similar differences in vertical distributions among species have been observed in light-trapped scarabaeid and meloid beetles in the Bornean rainforest (KATO *et al.*, 2000). Taken together, these findings indicate the existence of niche differentiation in a vertical forest structure among beetle species. Among *Endaenidius* species, *E. kemae* preferred the canopy, while *E. maetoi* preferred the understory. Descriptions of these species suggest the diversity in characters of many species in the tropical rainforest (KOJIMA & MORIMOTO, 1995).

In tropical rainforests in Southeast Asia, which lack a distinct dry season, a wide variety of temporal patterns exist in insect seasonality; for example, seasonal, aseasonal and supra-annual fluctuations (KISHIMOTO-YAMADA & ITIOKA, 2015). In this study, the height and color preferences of flower-visiting weevils appeared to change seasonally. The weevils appeared to prefer high and yellow traps in March and August, when it was hotter and drier, compared to December (KUME *et al.*, 2011; KOBAYASHI *et al.*, 2013). This change in the preference did not correspond to the population fluctuation that the weevil abundance reduced in March. As general flowering did not occur during the trapping periods in this study, floral resources are not considered to have fluctuated markedly (KOBAYASHI *et al.*,

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2013). Consequently, variations in environmental conditions seem responsible for the changes in the preference, although the mechanisms underlying the changes are not clear. Long-term trapping is necessary to examine such seasonality in flower-visiting weevils (KISHIMOTO-YAMADA & ITIOKA, 2015).

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要 約

渡部美佳・永光輝義・市岡孝朗・Paulus MELENG・小島弘昭:ボルネオの熱帯雨林において訪花性誘引剤 を用いた衝突誘引式トラップで採集されたゾウムシ類 (鞘翅目ゾウムシ科)の種多様性と垂直分布. マレーシア,サラワク州のランビル国立公園の低地フタバガキ林において,訪花性誘引剤を取り付けた衝突 誘引式トラップを地上25-45 m と 2 m の高さに設置し,ゾウムシ科甲虫を採集した.合計5,121 個体のゾウ ムシが採集され,7 亜科 49 種に同定された.日本の和歌山県の温帯林におけるゾウムシ相 (溝田・今坂, 1997)と比べると,この熱帯雨林では個体数と種数が多く,個体数が多い種の優占度が高かった.この熱帯 雨林で採集されたゾウムシの個体数は低所より高所で多く,高所で採集される頻度は種によって異なってい た.これらの結果は,訪花性ゾウムシの種多様性は温帯林より熱帯雨林で高く,熱帯雨林におけるその垂直 分布が種間で異なることを示唆している.

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A part of the title of SHIMAMOTO, КОЛМА and NAGANO's paper on *Elytra*, *Tokyo*, new series, 7 (1): 235–237 should be corrected as follows:

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> Masahiro ÔHARA Editor