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Altitudinal patterns of abundances and parasitism in frugivorous drosophilids in west Java, Indonesia

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Running title: Altitudinal pattern of parasitism in drosophilids

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Abundances and parasitism rates of frugivorous drosophilid flies were studied in three localities at altitudes of 250-1350 m in and near Bogor, Indonesia. The drosophilid and parasitoid species were classified into four groups, low-altitude species, high-altitude species, species abundant at a mid-altitude location, and species occurring rather evenly from low to high locations. The *ananassae* and *immigrans* species groups were major drosophilids collected. All species of the *ananassae* species group were more abundant at lower altitudes, and the parasitism rate in this species group decreased with increasing altitude. Thus, the host abundance seems to affect the parasitism rate. On the other hand, the rate of parasitism in the *immigrans* species group showed no apparent relation with altitude or density, possibly due to that species of this species group varied in altitudinal distribution. It is also suggested that the diversity of drosophilid species affects the composition of parasitoid species.

Keywords: abundance; altitude; frugivorous drosophilids; Indonesia; parasitoids; tropics.

Introduction

The species diversity of and abundance of parasitoids attacking herbivore insects have been reported to show exceptional latitudinal patterns; i.e., they are more diversified and the parasitism rate is higher in the temperate regions compared to the tropics (Owen and Owen 1974; Hespendeide 1978; Hawkins et al. 1997; Hawkins 1994). However, it is still poorly understood why they show such patterns. To address this issue, studies on on the patterns along with other environmental gradients or in non-herbivorous insects could provide some clues. Péré et al. (2013) suggested in their meta-analyses that both parasitism rates and parasitoid species richness decreased with increasing elevation. In our previous studies on parasitoids attacking frugivorous drosophilids, on the other hand, the species diversity did not so much differ between the tropical, subtropical and temperate regions, and the parasitism rate was much higher in the tropics compared to the subtropical and temperate regions (Mitsui and Kimura 2010; Novković et al. 2012; Kimura and Suwito 2012). On the other hand, no information is available on the altitudinal pattern of parasitism in drosophilid flies, although a number of references have been published on the altitudinal distributions and temperature adaptations of drosophilid flies in the temperate regions (Kimura et al. 1978; Bächli 1979; Bächli & Burla 1992; Beppu et al. 1996; Mitsui et al. 2010). High-altitude temperate *Drosophila* species are usually heat-susceptible and are assumed to suffer high mortality in summer if they occur at low altitudes (Kimura et al. 1994; Beppu et al. 1996). In addition, some temperate species perform seasonal migration between low and high altitudes to avoid summer heat at low altitudes (Kimura and Beppu 1993; Beppu et al. 1996; Mitsui et al.

2010). In the tropics, however, there are few studies on the altitudinal distributions of drosophilid flies except for fragmental reports on their occurrence at different altitudes (Suwito et al. 2002).

In this paper, we report the altitudinal pattern of parasitism in frugivorous drosophilids in west Java, Indonesia, to find clues for understanding of how the parasitoid species diversity and the parasitism rate are determined. We have already reported the composition of frugivorous drosophilid flies and their parasitoids based on the trap collections using banana as bait at a low altitude location (Bogor: approximately 250 m in altitude) in west Java (Kimura and Suwito 2012). In addition, we have shown host use of these parasitoids based on laboratory experiments on host suitability and acceptance (Kimura and Suwito 2014). In this study, we carried out trap collections in two locations, Sukamantri (approximately 700 m) and Cibodas (approximately 1350 m), and analysed the altitudinal pattern of drosophilid distribution and parasitism together with previous data in Bogor. As a result, the drosophilid and parasitoid species varied in the altitudinal patterns of abundance. In addition, the abundance of host drosophilid species seems to affect the parasitism rate, whereas the diversity of hoar species seems to affect the parasitoid composition.

Materials and methods

Frugivorous drosophilid flies and their parasitoids were collected in wooded and domestic areas in Sukamantri and Cibodas near Bogor (6.6 °S, 106.5 °E; about 250 m in altitude) in west Java, Indonesia, and compared with those in Bogor (Kimura and Suwito 2012). Sukamantri is located about 10 km southwest of Bogor at an altitude of about 700 m on the slope of Mt. Salak (2211 m in altitude), and Cibodas is located about 25 km southeast of Bogor at an altitude of about 1350 m on the slope of Mt. Gede (2958 m). Wooded sites in Sukamantri and Cibodas were located near the edges of dense forests, whereas a wooded site in Bogor was located in a grove in the Bogor Botanical Garden surrounded by town. It was difficult to find dense forests at low altitudes in west Java because of land development for agriculture, industry or residence. Domestic sites in Sukamantri and Cibodas were located in bushes in rural environments, while a domestic site in Bogor was located at the immediate vicinity of houses in the Bogor Botanical Garden. Monthly mean temperature ranges from 25.1 to 26.1 °C in Bogor and 20.4 to 24.2 °C in Cibodas. No climatic data were available for Sukamantri. From altitude, daily mean temperature in Sukamantri is estimated to be 23-24 °C.

Collections were carried out in three seasons (August and October in 2010 and March in 2011) in Sukamantri and two seasons (June and December in 2011) in Cibodas, whereas four seasons (June and September in 2008 and January and April in 2009) in Bogor (Kimura and Suwito 2012). Adult drosophilid flies were collected with traps baited with banana (about 30 g) added with dry yeast. One trap was set in each of forest and domestic environments at each locality. Adult drosophilid flies attracted to the traps were collected by net sweeping three times (morning, afternoon and evening) on the next day of trap setting in Sukamantri and Cibodas and on the next two successive days in Bogor in each collecting occasion (season).

For collections of parasitoids, three traps baited with banana (each trap baited with about 30 g banana) were set in each environment at the same time when collections of adult drosophilid flies were carried out. In this collection, dry yeast was not added to banana to avoid excessive fermentation. Five days after trap setting, banana baits in traps were brought back to the laboratory and placed in plastic boxes with tissue paper (banana baits in three traps were treated together). If banana baits were left longer, they decreased in quantity considerably and became unattractive to drosophilids probably due to excess fermentation. When drosophilid larvae in banana baits pupated, they were collected in Petri dishes with wet paper. Pupae were classified into three groups by morphology, 1) the *eugracilis-takahashii* type, 2) the *ananassae* type and 3) the *immigrans* type. For each type, pupae were collected up to 200 at each time in each environment. Thus, the present parasitism data are qualitative. Flies or parasitoids that emerged from the pupae were collected and identified.

To determine the altitudinal patterns of abundances of drosophilid flies, regression analysis was performed. In this analysis, the differences by season and environment were not taken into consideration, because collections were conducted in different seasons in different localities and conditions of collection sites may differ by locality. In the analysis, the number of flies of each species collected at each site per day in each season was log-transformed after addition of 1, i.e., log(N+1). When regression of the fly abundance on altitude was not significant (P>0.05), ANOVA was performed to determine whether the abundance is significantly different among the three locations (i.e., significantly more or less abundant at the mid-altitude location, Sukamantri).

To examine the effects of altitude and host abundance on parasitism, regression analysis was performed with the parasitism rate of each pupa-type group at each site in each season as a dependent variable and altitude or the abundance of (i.e., the log-transformed individual number of all species belonging to) each pupa-type group in the adult collections as a predictor variable.

The analysis was performed using Jmp ver. 6.1 (SAS Institute, Cary, USA).

Results

The individual number of common drosophilid species collected per trap per day per collecting occasion (season) at wooded and domestic sites in Bogor, Sukamantri and Cibodas are shown in Table 1. Females of the *ananassae* and *bipectinata* species complexes and the *nasuta* species subgroup were not identified to species because of difficulty of identification by morphology. According to the regression analysis and ANOVA without Bonferroni correction, these drosophilid species were classified into four groups, 1) species that were significantly more abundant at lower locations, 2) those that were significantly more abundant at higher locations, 3) those that were significantly more abundant at the mid-altitude location (Sukamantri), and 4) those occurring rather evenly from low to high locations. When sequential Bonferroni correction was applied, regression was significant ($P<0.05$) only in the six species (Table 1). Among the low-altitude species, *D. ananassae*, *D. atripex* and *D. bicornuta* were collected only in Bogor. Among the high-altitude species, *D. rhopaloa* and *D*. sp.

aff. *ustulata* were mostly collected in Cibodas.

Thirteen species of parasitoids were collected (Table 2). Among them, *Trichopria*, *Spalangia* and *Tachinaephagous* species are pupal parasitoids, while the others are larval parasitoids. Pupal parasitoids were not frequent in this survey, because most of the drosophilid individuals in the baits were still larvae at the time of collection.

Among larval parasitoids that emerged from *ananassae*-type pupae, *Leptolamina* sp. BG1 aff. *ponapensis* was almost restricted in Bogor, while *Asobara pleuralis* and *Leptopilina victoriae* were distributed to higher altitudes (Table 2). The overall parasitism rate of pupae of this type significantly (P<0.001) decreased with increasing altitude and also with decreasing fly abundance (i.e., the total number of adult flies belonging to the *ananassae* species group in the adult collections: Table 1) (Fig. 1). The total number of adult flies of this species group also significantly decreased with increasing altitude (P<0.001).

Among larval parasitoids that emerged from *immigrans*-type pupae, *A. pleuralis*, *Leptopilina pacifica* and *Leptolamina* sp. BG1 aff. *ponapensis* were more frequent at lower altitudes, while *A. orientalis* (cited as *Asobara* sp. BG1 in Kimura and Suwito, 2012) was more frequent at higher altitudes (Table 2). The overall parasitism rate of pupae of this type was somewhat higher at lower altitudes, but the effect of altitude or fly abundance (i.e., the total number of adult flies belonging to the *immigrans* species group in the adult collections: Table 1) on the parasitism rate was not significant (P=0.146 on altitude and P=0.275 on fly abundance: Fig. 1). In addition, no significant effect of altitude was observed on the total number of adult flies of this species group

(*P*=0.78).

Drosophila eugracilis was frequently parasitized by *A. pleuralis* at Bogor where this drosophilid was abundant, but scarcely parasitized at Sukamantri or Cibodas where it was less abundant (Tables 1 & 2). As well, *Drosophila* sp. aff. *takahashii* was frequently parasitized by *Ganaspis xanthopoda* at Cibodas where this drosophilid was abundant, but scarcely parasitized at Sukamantri where it was less abundant (Tables 1 & 2). Statistical analysis was not performed on these *Drosophila* species because sample size was small.

Drosophilid flies that emerged from banana were shown in Table 3. Among the species that were abundant or common in the adult collection (Table 1), about a half did not emerge from banana baits.

Discussion

The present drosophilid and parasitoid species showed species-specific altitudinal patterns of abundances (Table 1). In addition to altitude, environmental conditions of collecting sites would have some effects on their abundances. For example, *S. dorsocentralis*, *D. bipectinata*, *D. malekotliana* and *D. hypocausta* are abundant in a wooded site in Bogor (250 m in altitude) and domestic sites in Sukamantri (700 m) and/or Cibodas (1350 m). The wooded site in Bogor was located in a grove in town, and the domestic sites in Sukamantri and Cibodas were located in bushes in rural environments. Groves and bushes may be similar in physical conditions such as light regime or humidity, and the above drosophilid species may prefer such environments. In addition, the closeness of these sites to human habitation may be responsible. In human habitation, fruits and fruit wastes on which the present drosophilid species breed would be rather constantly supplied throughout a year due to consumption and cultivation by human, whereas fruit supply in natural areas would fluctuate seasonally. Such difference may have resulted in the difference in seasonality and abundances of these flies between domestic and wooded areas.

One of the major factors affecting altitudinal abundances of flies and parasitoids would be temperature. High-altitude *Drosophila* species are usually heat susceptible, and it is assumed that high-temperature conditions at low altitudes prevent them to expand their distributions to low-altitude areas (Kimura and Beppu 1993; Kimura et al. 1994; Beppu et al. 1996; Goto et al. 1999; Sultana et al. 1999). On the other hand, the present low-altitude drosophilid and parasitoid species can be maintained at 23 °C, an average temperature of Cibodas (Kimura and Suwito 2014). Thus, temperature does not directly limit the occurrence of low-altitude species at high altitudes but it may affect the occurrence in association with other factors such as competition or predation.

Interspecific competition is often assumed as a cause of altitudinal replacement of closely related bird species (Terborgh 1971; MacArthur 1972; Terborgh and Weske 1975; Remsen and Graves 1995), although there are some questions on this interpretation (Cadena & Loiselle 2007; Dhondt 2011). Resource competition could occur among the present drosophilid species, since they are basically fruit-feeders and at least a half of them breed on banana. In the present survey, altitudinal replacement was observed between *D*. sp. aff. *ustulata* and *D*. sp. aff. *formosana* of the *immigrans* species subgroup and between *D. eugracilis* and *D. takahashii*. However, it is not certain whether competition affects their replacement or not. At least in the studies of Shorrocks and Sevenster (1995) and Wertheim et al. (2000), interspecific competition is suggested to be not important as a factor structuring *Drosophila* communities.

If parasitism lowers the abundance of host species and limits their distribution, the parasitism rate must be high in areas where the host abundance is low. In the *ananassae* species group, *D. eugracilis* and *D. takahashii*, however, the parasitism rate was lower in localities where their abundances were low. In addition, no significant relation was observed between the abundance and the parasitism rate in the *immigrans* species group. Thus, parasitism did not directly limit the altitudinal distributions of drosophilid flies.

All species of the *ananassae* species group were more abundant at lower altitudes, and the parasitism rate in this species group was also higher at lower altitudes. Thus, the host abundance seems to have affected the parasitism rate. However, it is still possible that low temperatures or habitat characteristics at higher altitudes are unfavourable for both host *Drosophila* species and their parasitoids, and also that high-altitude populations of parasitoids have lost virulence against *Drosophila* species that are not frequent at high altitudes.

In contrast to the species of the *ananassae* species group, species of the *immigrans* species group varied in the altitudinal distribution. Therefore, even if each species shows a density-dependent parasitism, such relation would be masked in the present study, because the parasitism rate was determined at the level of species group due to the lack of diagnoses for the identification of species by puparium morphology. For further understanding, analyses at the species level are needed. Molecular approach may enable identification at the species level for both host puparia and parasitoids occurring in them.

It has been suggested that the effect of host abundance or density on the parasitism considerably varies due to variations in parasitoid behavior, distribution pattern of hosts, and spatial scale of sampling (Stiling 1987; Walde and Murdoch 1988). In this study, no apparent relation was observed between the host abundance and the parasitism rate at the location level (i.e., between sites within a location) even in the *ananassae* species group. The parasitism rate of these drosophilid flies may be determined at a relatively large spatial scale, i.e., at a between-location scale, not at a between-site scale within a location. Knowledge on dispersion of drosophilids and parasitoids would also be important to understand how the parasitism rate is determined.

The number of larval parasitoid species attacking the *ananassae* species group was 2 in Cibodas but 3 in Bogor and Sukamantri where this species group was more abundant (Tables 1 and 2). It is widely accepted that abundant host species support more parasitoid species (Hawkins 1994; Sheehan 1994; Stireman & Singer 2003). However, the number of parasitoid species attacking the *immigrans* species group was fewer in

Cibodas (2 compared with 5 in Bogor and Sukamantri), although the abundance of this species group did not so much differ between Cibodas and Bogor. In Cibodas, *Asobara pleuralis* and *Leptolamina* sp. BG1 did not emerge from the *immigrans* species group, whereas these two parasitoid species abundantly emerged from the *ananassae* and *immigrans* species groups in Bogor. The occurrence of a variety of host species may be important for the prevalence of such generalist parasitoid species. In Cibodas where the *ananassae* species group is much less frequent, these parasitoids may be inferior in competition with *A. orientalis* that is specialized to the *immigrans* species group. Thus, the diversity of host species may have affected the composition of parasitoid species through competitive interactions of parasitoids.

Thus, the abundance of host drosophilid species seems to affect the parasitism rate, and the host drosophilid diversity may affect the parasitoid composition. For further understanding, it is needed to investigate associations of drosophilid and parasitoid species (i.e., virulence of parasitoids and resistance of host drosophilids), and their adaptations to antagonists from different altitudes. According our study on host use of some parasitoids *(A. pleuralis*, *L. victoriae*, *A. pacifica* and *Leptolamina* sp. BG1 aff. *ponapensis*) from Bogor (Kimura and Suwito 2014), both parasitoid virulence and host resistance have species-specific components. In addition, some of drosophilid and parasitoid species showed geographic variation in resistance or virulence. Moreover, Seyahooei et al. (2011) observed a genetic differentiation between *Leptopilina boulardi* (Barbotin, Carton & Kelmer-Pillault) populations from different altitudes in Iran, although it was not examined whether virulence also differed between them. However, information on these issues is still limited.

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Table 1. Numbers of common drosophilid flies collected per trap per day per collecting occasion (season) at wooded (W) and domestic areas (D) in Bogor (altitude 250 m), Sukamantri (700 m) and Cibodas (1350 m) with results of of regression analysis (R) and ANOVA. ANOVA is performed when regression is insignificant *(P*>0.05). The distribution pattern (PD) is determined according to regression analysis and ANOVA: low-altitude species (L), high-altitude species (H), mid-altitude species (M) and species that occurs rather evenly (E).

	Bogor		Sukamantri		Cibodas		R	ANOVA	DP
	W	D	W	D	W	D			
No. of collecting occasion (season)	4	4	3	3	2	2			
No. of days of collection in a month	2	2	1	1	1	1			
Scaptodrosophila & *Zaprionus*									
Sc. dorsocentralis Okada	23.1	7.3	14.7	29.3	0.0	0.5	*P*=0.013	-	L
Sc. lurida Walker	1.1	0.1	4.7	4.7	0.0	0.0	*P*=0.793	*P*=0.069	E
Sc. sp. aff. *nigrofemorata*	1.9	0.0	0.3	0.3	0.0	0.0	-	-	
Zaprionus obscuricornis (Meijere)	1.6	0.1	56.7	32.7	1.5	1.5	*P*=0.582	*P*=0.001	M
Z. bogoriensis Mainx	2.6	1.4	71.3	42.0	0.5	4.5	*P*=0.793	*P*=0.156	E
Z. sp. SK1	0.0	0.0	25.0	6.0	0.0	0.0	*P*=0.667	*P*=0.031	M
The *melanogaster* species group									

The *bipectinata* species complex of the *ananassae* species subgroup									
D. bipectinata complex ♀	97.4	18.1	8.3	59.3	1.0	8.5			
D. bipectinata Duda ♂	49.5	7.9	0.3	27.7	0.0	0.0	*P*=0.003	-	L
D. parabipectinata Bock ♂	3.0	4.8	0.0	0.7	0.0	0.5	*P*=0.004	-	L
D. pseudoananassae Bock & Wheeler ♂	45.3	5.5	2.0	2.0	0.0	0.5	*P*=0.015	-	L
D. malekotliana Parshad & Paika ♂	73.0	5.3	9.7	38.7	0.0	12.0	*P*=0.04	-	L
The *ananassae* species complex of the *ananassae* species subgroup									
D. ananassae complex ♀	8.1	15.3	0.0	0.0	0.0	0.0			
D. atripex Bock & Wheeler ♂	7.6	14.5	0.0	0.0	0.0	0.0	*P*<0.001*	-	L
D. ananassae Doleschall ♂	0.6	6.8	0.0	0.0	0.0	0.0	*P*=0.007	-	L
The *montium* species subgroup									
D. bicornuta Bock & Wheeler	6.6	1.8	0.0	0.0	0.0	0.0	*P*=0.002*	-	L
D. barbarae Bock & Wheeler	1.5	0.0	0.0	0.7	0.0	0.0	-	-	
D. parvula Bock & Wheeler	0.0	0.0	21.3	0.0	51.5	10.5	*P*<0.001*	-	H
D. baimai Bock & Wheeler	0.0	0.0	5.7	0.7	20.5	1.0	*P*=0.004	-	H
The *eugracilis, rhopaloa & takahashii* species subgroups									
D. eugracilis Bock & Wheeler	64.9	9.5	1.3	1.0	0.0	3.5	*P*<0.001*	-	L
D. rhopaloa Bock & Wheeler	0.0	0.0	0.0	0.0	37.0	1.0	*P*=0.005	-	H
D. sp. aff. *takahashii*	0.0	0.0	2.7	3.0	13.0	51.0	*P*<0.001*	-	H
The *immigrans* species group									
The *nasuta* species subgroup									

D. nasuta subgroup ♀	35.8	6.1	17.0	12.0	2.5	3.0			
D. sulfurigaster albostrigata Wheeler ♂	50.0	5.1	22.3	13.0	0.5	0.5	*P*=0.01	-	L
D. kepulauana Wheeler ♂	8.8	0.5	8.7	1.3	3.5	3.0	*P*=0.876	*P*=0.926	E
D. kohkoa Wheeler ♂	0.0	0.0	0.0	0.0	2.5	0.0	-	-	
The *hypocausta* species subgroup									
D. hypocausta+siamana ♀	27.3	4.1	15.7	29.7	1.0	9.0			
D. hypocausta Osten-Sacken ♂	39.3	4.4	11.7	26.0	0.0	9.5	*P*=0.108	*P*=0.238	E
D. siamana Hihara & Lin ♂	0.0	0.0	25.3	32.0	5.5	6.0	*P*=0.059	*P*=0.001	M
D. neohypocausta Lin & Wheeler	0.0	0.0	3.0	0.7	0.0	0.0	-	-	
The *immigrans* species subgroup									
D. ruberrima Meijere	0.4	0.0	15.7	1.7	0.0	0.0	*P*=0.847	*P*=0.082	E
D. sp. aff. *formosana*	0.3	0.0	13.0	10.0	0.0	0.0	*P*=0.759	*P*<0.001	M
D. sp. aff. *ustulata*	0.0	0.0	0.0	0.3	31.0	27.5	*P*<0.001*	-	H
others	2.8	1.0	3.7	2.0	4.5	3.0			
Total	552.3	119.4	360.0	377.3	176.0	156.5			

* Regression is significant (*P*<0.05) even after sequential Bonferroni correction.

Table 2. Numbers of pupae of the *ananassae*, *eugracilis-takahashii* and *immigrans* types collected in Bogor, Sukamantri and Cibodas, and number of flies and wasps eclosed from those pupae. Number of pupae from which neither fly nor wasp emerged (dead pupae) and parasitism rate were also given.

	No. of pupae collected	No. of dead pupae	No. of flies	No. of wasps											Parasitism rate
				Ap	Ao	Lv	Lp	Lr	Lm	Gx	Tr	Ta	O	Total	
ananassae type pupae															
Bogor															
Wooded area	790	315	100	51	-	196	-	-	94	-	25	9	-	375	0.789
Domestic area	822	259	199	22	-	226	-	-	82	-	34	-	-	364	0.647
Sukamantri															
Wooded area	174	17	130	25	-	2	-	-	-	-	-	-		27	0.172
Domestic area	496	45	272	55	-	120	-	-	3	-	1	-	1	179	0.397
Cibodas															
Wooded area	54	1	50	1	-	2	-	-	-	-	-	-	-	3	0.057
Domestic area	139	5	112	8	-	13	-	-	-	-	-	-	-	21	0.158
eugracilis-takahashii type pupae															

Bogor															
Wooded area	143	38	59	40	-	-	-	-	-	3	-	2	1	46	0.438
Domestic area	70	38	28	3	-	-	-	-	-	-	1	-	-	4	0.125
Sukamantri															
Wooded area	157	32	116	-	-	-	-	-	-	-	-	8	1	9	0.072
domestic area	274	26	247	-	-	-	-	-	-	1	-	-	-	1	0.004
Cibodas															
Wooded area	253	25	221	-	-	-	-	-	-	6	-	-	1	7	0.031
Domestic area	290	52	177	-	-	-	-	-	-	62	-	-	-	62	0.259
immigrans type pupae															
Bogor															
Wooded area	378	39	94	59	15	-	45	6	109	-	-	8	3	242	0.720
Domestic area	154	65	32	13	4	-	5	6	29	-	-	-	-	57	0.640
Sukamantri															
Wooded area	440	80	161	65	103	-	14	2	3		-	12	-	199	0.553
Domestic area	116	7	64	11	25	-	9	-	-		-	-	-	45	0.413
Cibodas															
Wooded area	261	6	130	0	109	-	-	9	-	-	7	-	-	125	0.490
Domestic area	123	4	71	0	48	-	-	-	-	-	-	-	-	48	0.403

Wasp species: *Asobara pleuralis* (Ashmead) (Ap), *A. orientalis* Viereck (Ao: cited as *Asobara* sp. BG1 in Kimura and Suwito 2012), *Leptopilina victoriae* Nordlander (Lv), *L. pacifica* Novković & Kimura (Lp), *L. ryukyuensis* Novković & Kimura (Lr), *Leptolamina* sp. BG1 aff. *ponapensis* (Lm), *Ganaspis xanthopoda* (Ashmead) (Gx), *Trichopria* sp. BG1 (Tr), *Tachinaephagous* sp. BG1 (Ta), and others (O: *Asobara* sp. SK1, *Leptopilina* sp. BG1, *Leptopilina* sp. CB1 and *Spalangia* sp. SK1).

Table 3. Number of drosophilid flies that emerged from pupae of the *eugracilis-takahashii*, *ananassae* and *immigrans* types collected in Bogor, Sukamantri and Cibodas

	Bogor	Sukamantri	Cibodas
The *eugracilis-takahashii* type			
D. eugracilis	87	265	12
D. takahashii		95	384
unidentified			2
The *ananassae* type			
The *bipectinata* complex, female	65	240	88
D. bipectinata male	38	32	10
D. parabipectinata male	3		
D. pseudoananassae male	8	18	5
D. malekotliana male	17	111	59
The *ananassae* complex, female	66	1	
D. atripex male	63		
D. ananassae male	1		
S. dorsocentralis	7		
unidentified	21		
The *immigrans* type			
The *nasuta* subgroup, female	77	100	20
D. sulfurigaster male	32	59	18
D. kepulauana male	16	20	35
D. kohkoa male		1	1
D. siamana		22	42
D. neohypocausta		2	
D. formosana		21	2
D. ustulata			47
Z. bogoriensis	1		

Data from wooded and domestic areas are pooled.

Figure legend

Figure 1. Effects of host abundance on the parasitism rate in the *ananassae* (A) and *immigrans* species groups (B).

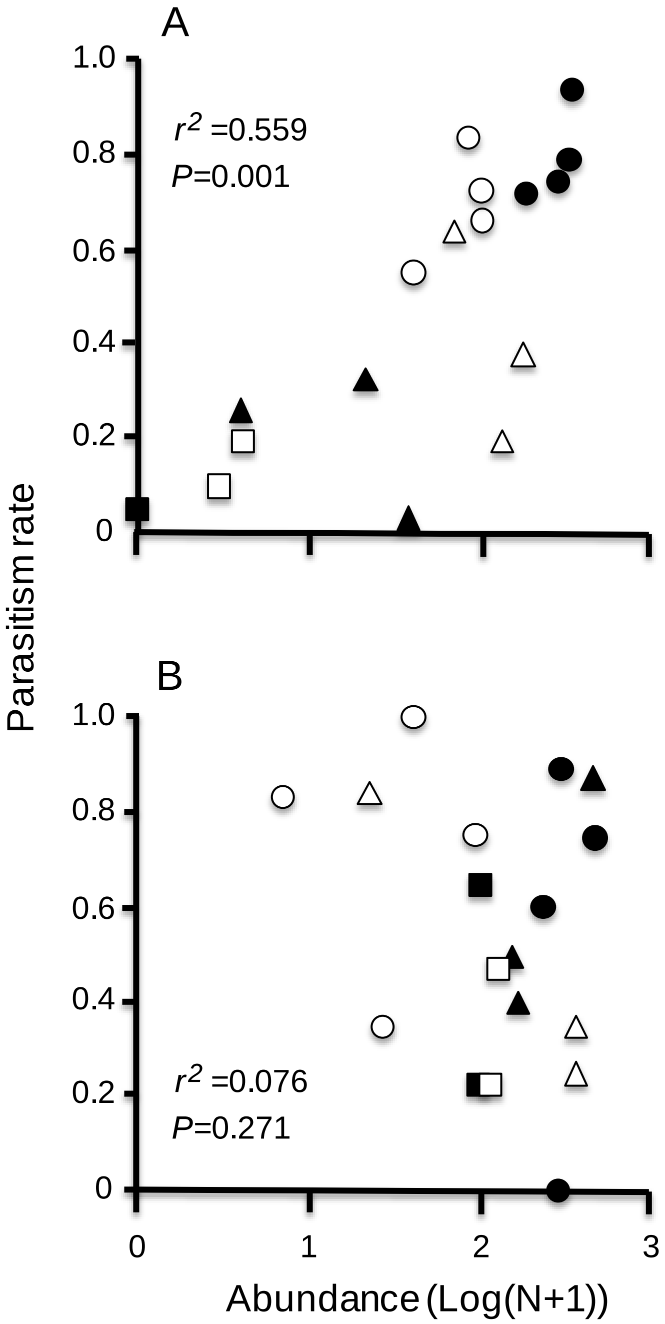
A
1.0
0.8
0.6
0.4
0.2
0
r^2 =0.559
P=0.001
Parasitism rate
B
1.0
0.8
0.6
0.4
0.2
0
r^2 =0.076
P=0.271
0
1
2
3
Abundance (Log(N+1))

Fig. 1