Diversity and abundance of frugivorous drosophilids and their parasitoids in Bogor, Indonesia

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Abstract

The diversity, abundance and association of frugivorous drosophilids and their parasitoids were studied in Bogor, Indonesia (the tropical region), and compared with the results in Iriomote-jima (the subtropical region) and Tokyo (the temperate region). In the collections of adult drosophilid flies by traps baited with banana in wooded areas, the number of commonly observed frugivorous drosophilid species (i.e. species that occupied more than 0.5% of total drosophilid samples) was 10 in Bogor and nine in Iriomote-jima, more than in Tokyo (six species), probably reflecting the high diversity and abundance of fruits. The rate of parasitism was very high in Bogor, especially in species of the *Drosophila ananassae* and *immigrans* species groups. The diversity of parasitoids attacking frugivorous drosophilids was higher in Bogor and Iriomote-jima than in Tokyo, possibly due to the high species diversity of host drosophilids. Parasitoids generally showed wider latitudinal distributions than drosophilids. No remarkable difference was observed in the host range among tropical, subtropical and temperate parasitoids.

Keywords: Abundance, association, Bogor, diversity, frugivorous drosophilids, host range, parasitoids, tropics.

Introduction

The species diversity of most groups of animals, plants and microorganisms increases toward tropics (Huston 1994; Hillebrand 2004; Huggett 2004), and a number of hypotheses have been proposed to explain this latitudinal gradient (Turner and Hawkins 2004; Mittelbach et al. 2007). One of explanations is the high diversity and abundance of resources available in the tropics (Huston 1994; Huggett 2004; Turner and Hawkins 2004). In addition, it is often suggested that ecological niches become narrower and species are more specialized in the tropics, leading to the coexistence of a larger number of species even within the same resource space (Huston 1994; Huggett 2004; Turner and Hawkins 2004). The narrower niches in the tropics are considered to be attributable to severe competition and the stable resource availability relying on the stable climatic conditions (Connell and Orias 1964; Huggett 2004). In some groups of parasitoid insects, on the other hand, the species diversity is known to decrease towards tropics (Owen & Owen 1974; Hespendeide 1978; Hawkins et al. 1992; Bartlett et al. 1999), but its reason is uncertain. Here, we studied the diversity, abundance and association of frugivorous drosophilids and their parasitoids in Bogor, Indonesia, and compared their diversities with those in the subtropical and temperate regions.

Drosophilid flies and their parasitoids have often been used as a model system in the study of evolution and bio-diversification under antagonistic interactions (Nappi et al. 2009; Dubuffet et al. 2009; Dupas et al. 2009; Kraaijeveld and Godfray 2009). It has been well documented that the species diversity of drosophilid flies is much higher in the tropics than in the temperate regions (Wheeler 1981; Bächli and Rocha Pité 1981; Val et al. 1981; Tsacas et al. 1981; Okada 1981). In contrast, there is limited knowledge on the diversity of *Drosophila* parasitoids, especially in the Asian tropics. Here, we focus on frugivorous drosophilids and their parasitoids, since a number of studies have been conducted on parasitoids attacking frugivorous drosophilids in Europe and Japan (Carton et al. 1986; Janssen et al. 1988; Fleury et al. 2004, 2009; Ideo et al. 2008; Mitsui et al. 2007; Mitsui and Kimura 2010). The diversity of parasitoids attacking drosophilid flies of other niches has been little studied even in the temperate regions (Driessen et al. 1990; Yorozuya 2006).

Methods

Frugivorous drosophilid flies and their parasitoids were collected four times in 2008 (June and September) and 2009 (January and April) in wooded areas and around houses in the Bogor Botanical Garden, Bogor (6.6 °S, 106.5 °E), Indonesia. Collections of adult drosophilid flies were carried out with traps baited with fermenting banana (each trap baited with about 30 g banana added with dry yeast). Two traps were set in each environment, and adult flies attracted to traps were collected by net sweeping three times in a day (morning, afternoon and evening). Collection was carried out for two successive days after the trap setting.

Collections of parasitoids in drosophilid larvae growing in banana were also carried out. Four traps baited with banana (each trap baited with about 30 g banana) were set in each of the two environments, wooded areas and around houses. In this collection, dry yeast was not added to banana, since the addition excessively facilitates fermentation. After 5 days, banana in the traps was brought back to the laboratory and placed in plastic boxes with tissue paper. When drosophilid larvae in banana pupated, they were collected in Petri dishes with wet paper. Pupae were classified into three groups by morphology, 1) the *eugracilis* type, 2) the *ananassae* type and 3) the *immigrans* type. For each type, pupae were collected up to 200 for each environment. Flies or parasitoids that emerged from the pupae were collected and identified.

In drosophilids, females of each of the *bipectinata* species complex, the *ananassae* species complex and the *nasuta* species subgroup were treated together, since they are hardly distinguishable (Table 1). Identification of parasitoids usually relied on morphology but sometimes on nucleotide sequences of the "cytochrome oxidase subunit 1" gene and the internal transcribed spacer 2 (Schilthuizen et al. 1998; Novković et al. 2011; Kasuya et al. submitted).

RESULTS

Table 1 shows the number of adult flies of drosophilid species collected by banana traps in wooded areas and around houses in the Bogor Botanical Garden. The species of the *bipectinata* complex represented 46 % of total drosophilids, the species of the *ananassae* complex did 8 %, the species of the *nasuta* species subgroup did 16 %, and

D. eugracilis did 11%. Most species were collected more frequently in wooded areas than around houses, but *D. ananassae*, *D. parabipectinata* and *D. atripex* were more frequently collected around houses. In wooded areas, *D. bipectinata* was abundantly collected in September and January, and *D. pseudoananassae* and *D. eugracilis* were in April and June, but their seasonality was not clear around houses. Other species showed less clear seasonality.

Tables 2 and 3 show the number of pupae collected from banana placed in wooded areas and around houses, respectively. Pupae of the *ananassae* type were abundantly collected throughout year in both environments, while pupae of the *eugracilis* type were not so abundant except in June in wooded areas. Pupae of the *immigrans* type were more abundantly collected in wooded areas. In wooded area, they were more abundant in June and January than in September and April.

Table 4 shows the composition of drosophilid flies that emerged from pupae of each type. Pupae of *S. dorsocentralis* were included in the *ananassae* type, and those of *Z. bogoriensis* were included in the *immigrans* type. From pupae of the *immigrans* type, *D. hypocausta* did not emerged, although adult flies of this species were rather abundantly collected (Table 1).

Ten parasitoid species emerged from the pupae collected in Bogor. Among them, four species, *Asobara pleuralis* (Ashmead), *Leptopilina victoriae* Nordlander, *L. pacifica* Novković & Kimura and *Leptolamina* sp. BG1 aff. *ponapensis*, were rather frequent. The rate of parasitism was usually very high in the *ananassae* and *immigrans* types, but not so high in the *eugracilis* type.

Asobara pleuralis emerged from all of the three types, while *Asobara* sp. BG1 emerged only from the *immigrans* type. *Leptopilina victoriae* emerged only from the *ananassae* type, *L. ryukyuensis* Novković & Kimura and *L. pacifica* from the *immigrans* type, *Ganaspis xanthopoda* (Ashmead) from the *eugracilis* type, and *Leptolamina* sp. BG1 from the *ananassae* and *immigrans* types. *Tachinaephagus* sp. BG1 emerged from all of the types, and *Trichopria* sp. BG1 mainly from the *ananassae* type. However, the restriction of *Asobara* sp. BG1, *L. ryukyuensis*, *G. xanthopoda*, and *Trichopria* sp. BG1 to either of *Drosophila* groups could be a bias due to the small sample size (Tables 2 & 3).

Discussion

Diversity and abundance of drosophilid flies

To clarify the latitudinal pattern in species diversity, drosophilid flies collected by traps in wooded areas are compared among Bogor (the tropical region: 6.6 °S), Iriomote-jima (the subtropical region: 24.3 °N) and Tokyo (the temperate region: 36.7 °N). In Iriomote-jima and Tokyo, collection was carried out using retainer-type traps baited with banana throughout a year (Hirai et al. 2000; Beppu 2006). In Bogor, 4418 individuals belonging to 30 species were collected in wooded areas, and 11 of the 30 species were rather common (species that comprised more than 0.5 % of total drosophilid flies were tentatively assigned as common). In Iriomote-jima, 6142 individuals belonging to 25 species were collected in forests, and 14 of the 25 species were common (data at forest floor presented in Table 4 in Hirai et al. 2000). In Tokyo, 11443 individuals belonging to 29 species were collected in a deciduous-broad leaved forest, and 12 were common (data of II-D in Table 1 in Beppu 2006). The number of common species was also 12 in a sample at another forest site in Tokyo, although the number of collected individuals is more than two times (data of I-D in Table 1 in Beppu 2006). In the common species among these three localities, there is no overlap except *S. dorsocentralis* and *D. bipectinata* which commonly occur in Bogor and Iriomote-jima, probably due to the difference in their temperature tolerance (Kimura 2004). Although there is such a great difference in the species composition, the number of species collected, particularly the number of common species, differs little among these localities.

Although the number of common species did not differ so much among these localities, the proportion of fruit-feeders differed. Ten of the 11 common species in Bogor were frequently observed to breed on banana in this study. On the other hand, 9 of the 14 common species in Iriomote-jima and 6 of the 12 common species in Tokyo mainly breed on fruits including banana (Kimura et al. 1977; Nishiharu 1980; Hirai et al. 2000; Mitsui and Kimura 2010; Mitsui et al. 2010; Novković et al. submitted). In addition, among the 6 fruit-feeding species in Tokyo, three (*D. melanogaster, D. simulans* and *D. immigrans*) are introduced species that have origins in the tropics or subtropics (Tsacas et al. 1981; Okada 1981). Thus, native fruit-feeders are more species-rich in the tropics and subtropics, probably reflecting the high diversity and abundance of fruits.

On the other hand, the remaining common species in Iriomte-jima and Tokyo are generalists or mushroom-feeders (Nishiharu 1980; Hirai et al. 2000; Mitsui et al. 2010; Kasuya et al. submitted). In addition, the fruit-feeders in the temperate regions often breed on mushrooms or decayed leaves (Kimura et al. 1977; Nishiharu 1980; Kasuya et al. submitted). Niche may be wider in the temperate species.

There are some differences in habitat selection among drosophilids; *D. parabipectinata, D. atripex* and *D. ananassae* were more frequently collected around houses, while the others were more frequent in wooded areas. Among the first three, *D. ananassae* is a well-known domestic species (Parsons and Stanley 1981). It is not known what factors around houses are favorable for these domestic species. There are also some differences in seasonality; *D. bipectinata* was abundant in April and June but scarce in September and January, whereas *D. pseudoananassae* and *D. eugracilis* showed opposite trends. In general, temperature and precipitation are most important factors affecting the population dynamics of drosophilids. In Bogor, temperature is almost constant throughout year, while rainy season usually lasts from November until April in Bogor. It is possible that precipitation affects the population sizes of drosophilids, but it is not known why *D. bipectinata* and *D. pseudoananassae* or *D. eugracilis* showed the opposite tendencies in seasonality.

Among the common species in Bogor, the *ananassae* species group (*D. atripex* of the *ananassae* species complex, and *D. bipectinata, D. parabipectinata, D. pseudoananassae* and *D. malekotliana* of the *bipectinata* species complex), the *nasuta* species subgroup (*D. sulfurigaster* and *D. keplauana*) and *D. eugracilis* frequently emerged from banana placed in traps. The other common species may not prefer succulent, soft fruits like banana for breeding. There was some inconsistency in the seasonal trends between the collections of pupae and adult flies, but its reason was not known.

Diversity and abundance of parasitoids

Ten parasitoid species were confirmed to attack fruit-feeding drosophilid species in Bogor. Among them, *Trichopria* sp. BG1 is a pupal parasitoid, and the others except *Tachinaephagus* sp. BG1 are larval parasitoids. The host stage at which *Tachinaephagus* sp. BG1 attacks is not known. In larval parasitoids, *Asobara* sp. BG1, *L. ryukyuensis* and *L. pacifica* emerged only from the *immigrans* species group, *L. victoriae* from the *ananassae* species group, and *G. xanthopoda* from *D. eugracilis* of the *melanogaster* species group. On the other hand, *A. pleuralis* emerged from all of the *melanogaster*, *ananassae* and *immigrans* species groups, and *Leptolamina* sp. BG1 from the *ananassae* and *immigrans* species groups. Thus, at least some tropical parasitoids have rather wide host range. In this study, however, pupae of the *ananassae* and *immigrans* species groups could not be identified to species. To clarify the host-parasitoid associations at the species level, parasitism experiments using laboratory stocks of drosophilids and parasitoids are needed.

In these eight larval parasitoids, four were relatively frequent both in wooded areas and around houses. On the other hand, the number of frequent parasitoid species is 3-5 in Iriomote-jima and 2 in Tokyo (Mitsui et al. 2007; Mitsui and Kimura 2010; Novković et al. submitted), suggesting that the diversity of parasitoids attacking frugivorous drosophilids is lower in the temperate region than in the tropical and subtropical regions. The low number in Tokyo is due to the absence of parasitoids attacking the *immigrans* species group (Mitsui et al. 2007; Mitsui and Kimura 2010).

Among the eight larval parasitoids from Bogor, five (*Leptopilina victoriae*, *L. pacifica*, *L. ryukyuensis*, *Ganaspis xanthopoda* and *Asobara pleuralis*) are also recorded from Iriomote-jima, and one (*G. xanthopoda*) from Tokyo (Mitsui et al. 2007; Mitsui and Kimura 2010; Novković et al. 2011, submitted). Thus, these parasitoids have much wider distribution ranges than tropical drosophilids which scarcely occur in the subtropical and temperate regions. However, it is not known why there is such difference.

The rate of parasitism was very high (more than 80 %) in the *ananassae* and *immigrans* species groups, but not so high (about 50 %) in *D. eugracilis* (In the calculation of the parasitism rate, host pupae from which neither fly nor parasitoid emerged were excluded, since it was not known whether they were parasitized or not). In the temperate and subtropical regions, the parasitism rate was usually lower than 40 %, although it sometimes exceeds 80 % (Janssen et al. 1988; Fleury et al. 2004, 2009; Mitsui et al. 2007; Mitsui and Kimura 2010: Novković et al. submitted). Thus, parasitism would play an important role in the population dynamics of host drosophilids in the tropics and constitute an important selective force for the evolution of host resistance.

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Table 1. Number of adullt drosophilid flies collected by traps baited with fermenting banana from June 2008 to April 2009 in the Bogor Botanical Garden.

	Wooded areas				Around houses				Total
	Jun.	Sep.	Jan	Apr	Jun.	Sep.	Jan	Apr	
Scaptodrosophila dorsocentralis Okada	4	22	87	72	3	19	24	12	243
Sc. lurida Walker		9				1			10
Sc. sp. aff. *nigrofemorata*	8		6	1					15
Zaprionus obscuricornis (Meijere)	3	2	5	3			1		14
Z. bogoriensis Mainx	2	12	5	2			9	2	32
The *ananassae* species group									
The *bipectinata* species complex ♀	277	120	201	181	11	56	15	63	924
D. bipecitinata Duda ♂	35	128	169	64	3	40	6	14	459
D. parabipectinata Bock ♂	1	6	15	2	14	11	3	10	62
D. pseudoananassae Bock & Wheeler ♂	103	9	8	242	1	5		38	406
D. malekotliana Parshad & Paika ♂	227	102	134	121	4	18	1	19	626
The *ananassae* species complex ♀	30	9	20	6	54	21	21	26	187
D. atripex Bock & Wheeler ♂	23	10	16	12	46	24	28	18	177
D. ananassae Doleschall ♂	1	2	1	1	30	10	5	9	59
The *melanogaster* and *montium* species group									
D. eugracilis Bock & Wheeler	224	24	17	254	5	11		60	595

D. bicornuta Bock & Wheeler	22	15	11	5	2	6		6	67
D. barbarae Bock & Wheeler	4	1		7					12
The *immigrans* species group									
The *nasuta* species subgroup ♀	77	25	37	147	3	4	2	40	335
D. sulfurigaster albostrigata Wheeler ♂	63	70	78	189		8	5	28	441
D. kepulauana Wheeler ♂	22	11	12	25				4	74
D. hypocausta Osten-Sacken	146	189	97	100	3	27	19	19	600
Others*	8	5	6	8	3	2	1	2	35
Total	1280	771	925	1442	182	263	140	370	5373

* : *Sc. bryanai* Malloch, *Liodrosophila globosa* Okada *D. parapallidosa* Tobari, *D. melanogaster* Meigen, *D. serrata* Malloch, *D. ruberrima* Meijere, *D. polychaeta* Patterson & Wheeler, and undetermined species of *Amiota*, *Scaptodrosophila*, *Dichaetophora*, *Mulgravea* and the *immigrans* species group were included.

Table 2. Number of pupae of *D. eugracilis*, the *ananassae* species group, and the *immigrans* species group collected in wooded areas in the Bogor Botanical Garden, number of pupae from which neither fly nor wasp emerged (dead pupae), number of flies that emerged, and number of wasp species that emerged: *Asobara pleuralis* (Ap), *A.* sp. (As), *Leptopilina victoriae* (Lv), *L. ryukyuensis* (Lr), *L. pacifica* (Lp), *L.* sp. (Ls), *Ganaspis xanthopoda* (Gx), *Leptolamina* sp. (Ls), *Tachinaephagus* sp (Ta), *Trichopria* sp. (Tr), and the rate of parasitism (dead pupae were excluded from the calculation).

	No. of pupae collected	No. of dead pupae	No. of flies	Number of wasps											Rate of parasitism
				Ap	As	Lv	Lr	Lp	Ls	Gx	Lm	Ta	Tr	Total	
June 2008															
The *eugracilis* type	99	23	36	34					1	3		2		40	0.526
The *ananassae* type	206	93	7	13		44					40	9		106	0.938
The *immigrans* type	175	29	15	14			2	26	3		82	4		131	0.897
September 2008															
The *eugracilis* type	24	7	16	1										1	0.059
The *ananassae* type	225	92	38	11		55					27		2	95	0.714
The *immigrans* type	13	5	8											0	0
January 2009															
The *eugracilis* type	12	1	6	5										5	0.455
The *ananassae* type	173	44	33	23		53					19		1	96	0.744

The *immigrans* type	166	0	66	43	14		3	15	24	1		100	0.602
April 2009													
The *eugracilis* type	8	7	1									0	0
The *ananassae* type	186	86	22	4		44			8		22	78	0.780
The *immigrans* type	24	5	5	2	1		1	4	3	3		14	0.737

Table 3. Number of pupae of *D. eugracilis*, the *ananassae* species group, and the *immigrans* species group collected around houses in the Bogor Botanical Garden, number of pupae from which neither fly nor wasp emerged (dead pupae), number of flies that emerged, and number of wasp species that emerged, and the rate of parasitism. Abbreviations for wasp species, see Table 2.

	No. of pupae collected	No. of dead pupae	No. of flies	No. of wasps								Rate of parasitism
				Ap	As	Lv	Lr	Lp	Lm	Tr	Total	
June 2008												
The *eugracilis* type	3		2	1							1	0.333
The *ananassae* type	207	36	54	1		81			35		117	0.684
The *immigrans* type	52	10	7	4			3		28		35	0.833
September 2008												
The *eugracilis* type	10	4	6								0	0
The *ananassae* type	195	96	28	1		29			40	1	71	0.717
The *immigrans* type	2	1	0						1		1	1
January 2009												
The *eugracilis* type	13	2	9	2							2	0.182
The *ananassae* type	170	12	71	16		60			5	6	87	0.551
The *immigrans* type	55	21	22	7	4			1			12	0.353

April 2009											
The *eugracilis* type	44	32	11						1	1	0.083
The *ananassae* type	250	115	46	4	56			2	27	89	0.659
The *immigrans* type	45	33	3	2		3	4			9	0.750

Table 4. Number of drosophilid flies that emerged from pupae of the *eugracilis*, *ananassae* and *immigrans* types collected in wooded areas and around houses in Bogor. Data of different seasons are pooled.

	Wooded areas	Around houses
The *eugracilis* type		
D. eugracilis	59	28
The *ananassae* type		
The *bipectinata* complex, Female	39	26
D. bipecitinata Male	20	18
D. parabipectinata Male	-	3
D. pseudoananassae Male	4	4
D. malekotliana Male	12	5
The *ananassae* complex, Female	7	59
D. atripex Male	9	54
D. ananassae Male	-	1
S. dorsocentralis	3	4
unidentified	6	15
The *immigrans* type		
The *nasuta* subgroup, Female	58	19
D. sulfurigaster albostrigata Male	23	9
D. kepulauana Male	12	4
Z. bogoriensis	1	-